



Dynamique spatiale du charançon du bananier en interaction avec le système de culture et l'organisation paysagère

Fabrice Vinatier

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THÈSE

Présentée pour obtenir le grade de docteur délivré par

**L'Institut des Sciences et Industries
du Vivant et de l'Environnement**

(AgroParisTech)

Spécialité : Sciences agronomiques

Fabrice VINATIER

**Dynamique spatiale du charançon du bananier en interaction avec le
système de culture et l'organisation paysagère**

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AVANT-PROPOS

L'intensification des systèmes agricoles a profondément bouleversé les équilibres biologiques (Tilman et al. 2002). La monoculture et l'usage de produits phytosanitaires ont favorisé certaines populations de ravageurs. Les engrais et produits chimiques utilisés en agriculture intensive ont contribué à la pollution des cours d'eau, nappes phréatiques et sols. Le chlordécone, pesticide utilisé dans des zones de production bananière intensive en est un bon exemple (Cabidoche et al. 2009; Henriques et al. 1997). Cette molécule, utilisée pour la lutte contre le charançon du bananier en Martinique et en Guadeloupe à partir de 1972 (Vilardebo et al. 1974), a été interdite en 1993 du fait de sa toxicité et sa forte persistance et a été classée comme cancérigène possible chez l'homme dès 1979 (Multigner et al. 2010). Aujourd'hui, près de 20 ans après l'arrêt de son utilisation, la pollution des sols, des écosystèmes aquatiques et des denrées alimentaires doit encore être gérée. Le contrôle de ce ravageur par des méthodes alternatives (biologiques) représente un enjeu majeur de la durabilité de cette culture aux Antilles et dans toutes les zones de production bananière.

Les efforts de recherche en agronomie doivent à présent porter sur la compréhension des processus écologiques dans les agroécosystèmes afin notamment de limiter, voire de supprimer l'usage de certains insecticides. Les processus les plus importants sont basés sur les relations entre l'insecte et son environnement (Lewis et al. 1997). Or, dans le cas de certaines populations d'insectes ravageurs, la prise en compte de l'espace est essentielle à la compréhension des interactions entre population et environnement (Tilman and Kareiva 1997). L'ajout de cette nouvelle dimension nécessite l'usage d'outils originaux pour quantifier et analyser la dynamique spatiale des insectes en relation avec leur milieu (Cressie 1993b). Nous prendrons comme cas d'étude le charançon du bananier, ravageur majeur de cette culture et insecte marcheur avec des capacités de dispersion modérées, pour lequel les aspects spatiaux sont importants.

L'objectif principal de cette thèse est de comprendre les mécanismes affectant la distribution spatiale du charançon dans son environnement afin de s'en servir comme leviers pour limiter sa population. Le travail réalisé combine suivi sur le terrain d'insectes marqués et simulation par un modèle mécaniste individu-centré de la dynamique spatio-temporelle de la population. Il aborde le lien entre individu et population, entre les patterns spatiaux et les processus sous-jacents. Il repose sur la synthèse des données bibliographiques existantes sur l'écologie de l'insecte, ainsi que sur des résultats originaux d'expérimentations ciblées sur sa dynamique spatiale.

Toute la thèse s'organise autour de la conception d'un modèle mécaniste figurant la dynamique spatiale du charançon en relation avec son environnement. Le modèle est ici un outil de recherche pour identifier les mécanismes intervenant de façon essentielle dans la problématique étudiée. Un certain nombre d'hypothèses seront formulées sur les phénomènes

à considérer ou non, et la validité de ces hypothèses sera testée au regard de la fidélité du modèle à la réalité. Le modèle permet de mettre en évidence les carences dans nos connaissances pour définir des priorités dans la recherche et dans l'expérimentation. Le modèle est également un outil de prévision qui permet de prévoir le comportement du système modélisé dans différentes situations (Lett 1999).

Modèle mécaniste et statistiques sont des outils fondamentaux permettant de mener à bien l'objectif de la thèse. Chaque outil sera utilisé de manière itérative dans une démarche générale de compréhension d'un mécanisme écologique.

Ce travail a donné lieu à cinq publications (3 publiées, 1 soumise et 1 à soumettre), ainsi qu'à six présentations lors de congrès (3 communications orales et 3 posters):

PUBLICATIONS

- **Vinatier, F.**, Tixier, P., Le Page, C., Duyck, P.-F., Lescourret, F., 2009. COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. **Ecological Modelling** 220, 2244-2254.
- **Vinatier, F.**, Chailleux, A., Duyck, P.-F., Salmon, F., Lescourret, F., Tixier, P., 2010. Radiotelemetry unravels movements of a walking insect species in heterogeneous environments. **Animal Behaviour** 80, 221-229.
- **Vinatier, F.**, Tixier, P., Duyck, P.-F., Lescourret, F., 2010. Factors and mechanisms explaining spatial heterogeneity. A review of methods for insect populations. **Methods in Ecology and Evolution**, doi: 10.1111/j.2041-210X.2010.00059.x
- **Vinatier, F.**, Lescourret, F., Duyck, P.-F., Martin, O., Senoussi, R., Tixier, P., **soumis**. Should I stay or should I go? Habitat dependent kernel improves prediction of movement process. **The American Naturalist**
- **Vinatier, F.**, Lescourret, F., Duyck, P.-F., Tixier, P., **à soumettre**. From IBM to IPM: How to use individual-based models to design spatial arrangement of traps and crops. **Agriculture, Ecosystems & Environment**

COMMUNICATIONS

- **Oral: Vinatier, F.**, P. F. Duyck, G. Mollot, and P. Tixier. 2010. Spatial ecology of *Cosmopolites sordidus* in banana field landscapes. in Landscape management for functional biodiversity, pp. 139-142 IOBC, Cambridge, England.
- **Oral: Vinatier, F.**, 2009. COSMOS, a spatially explicit model for the epidemiology of banana weevil (*Cosmopolites sordidus*, Germar). Farming System Design 2009. Monterey, CA.
- **Oral: Vinatier, F.**, 2008. Modélisation spatialisée de l'épidémiologie du charançon du bananier en interaction avec le système de culture et l'organisation paysagère. Rencontres du CIRAD 2008, Montpellier.
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- **Poster: Vinatier, F.**, Tixier, P., Le Page, C., Bruchou, C., Duyck, P.-F., Lescourret, F., 2008. COSMOS, a spatially explicit model for the epidemiology of banana weevil (*Cosmopolites sordidus*, Germar.). In: IOBC (Editor), VIIème conférence IOBC sur la Production Fruitière Intégrée, Avignon, France.

CHAPITRE I –INTRODUCTION GENERALE

1. Comprendre l'hétérogénéité spatiale des populations d'insectes

Cette section aborde la notion d'hétérogénéité spatiale d'une population et définit l'ensemble des termes d'écologie spatiale utilisés dans mon travail de thèse. L'hétérogénéité spatiale d'une population est la résultante de facteurs intrinsèques à l'espèce, comme son mouvement et ses processus démographiques (mortalité et reproduction) (Turchin 1998), et de facteurs extrinsèques tels que la variation spatiale et temporelle de son environnement (Leyequien et al. 2007; Tscharncke et al. 2002). L'espace a longtemps été négligé en écologie des populations car en tenir compte complique grandement les études de terrain et les travaux de modélisation dans ce domaine (Tilman and Kareiva 1997). Cependant, l'intégration d'une composante spatiale a permis de comprendre des processus importants comme la coexistence entre proie et prédateur (Huffaker 1958) ou la distribution agrégée d'une population ayant de faibles capacités de dispersion (Tilman and Kareiva 1997).

Le *paysage* est une portion de région hétérogène composée d'une association particulière d'écosystèmes (Forman and Godron 1986). Il est composé d'une matrice d'éléments considérés comme homogènes pour une propriété donnée. Les propriétés des éléments seront choisies en fonction du processus écologique à expliquer. Dans la suite de la thèse, le paysage est considéré comme une portion de l'espace terrestre saisi horizontalement par un observateur et impliquant un point de vue. Les processus agissant à l'échelle de l'insecte, l'étendue du paysage désigné dans la thèse sera restreinte à la taille d'une parcelle de culture, chaque élément d'habitat faisant un mètre carré. Nous admettons que l'échelle choisie dans notre cas diffère de celle communément admise en écologie du paysage, qui considère une surface beaucoup plus large et occupant généralement plusieurs hectares. Le *processus* est désigné comme un ensemble de phénomènes, ou *mécanismes*, conçus comme actifs et organisés dans le temps. Dans la suite de la thèse, on désignera l'élément de paysage comme un *habitat* pour l'espèce considérée, le terme habitat étant pris ici au sens général pour indiquer un milieu ayant une influence positive ou négative, par opposition au sens premier du terme qui indique l'ensemble des milieux qu'une espèce utilise pour assurer ses fonctions vitales (Blondel 1995). Les termes *mouvement* et *dispersion* désigneront au sens large le processus de déplacement des individus dans l'espace (Begon et al. 1996), la distinction entre les deux termes étant variable suivant les auteurs (Huffaker and Gutierrez 1999).

L'*hétérogénéité spatiale* d'une population est définie par la variation dans l'espace d'un paramètre de cette population (Legendre and Legendre 1984), comme le nombre d'individus par unité de surface, ou la quantité de dégâts par plante engendrée par un insecte ravageur. On distingue trois types majeurs de distribution des individus dans l'espace: régulière, aléatoire ou agrégée (Begon et al. 1996). Ceux-ci ne représentent toutefois qu'une fraction de l'infinie

diversité des motifs spatiaux engendrés par la distribution d'une espèce donnée (Wiegand et al. 2009). On désignera par *pattern*¹ *spatial* n'importe quel motif ayant une structure spatiale non aléatoire et contenant des informations sur les mécanismes desquels il émerge. De manière plus générale, la définition de *pattern* sera étendue aux observations de toute sorte, issues ou non de données spatialisées et présentant une structure non aléatoire révélatrice d'un mécanisme écologique.

Il est nécessaire de définir la perspective spatiale, temporelle et organisationnelle adéquate afin de comprendre un processus spatial (Tilman and Kareiva 1997). La perspective choisie, avec ses propres échelles de temps et d'espace, agira comme un filtre sur le phénomène considéré (Fortin and Dale 2005). La *résolution spatiale* du filtre devra être suffisante pour capter les mécanismes en jeu, celle-ci étant définie par le rapport entre la zone d'observation (*étendue*) et la plus petite unité de surface (*grain*) de l'étude. La distribution des individus sera dépendante de la zone d'observation et du grain considérés (Lawson 2006). Cette définition de la résolution peut aisément s'étendre au temps (*résolution temporelle*) où le grain correspond au pas de temps entre deux observations et l'étendue la durée totale d'observation du phénomène spatial. De la même manière, la *résolution organisationnelle* considère comme zone d'observation les stades de développement de l'organisme considéré qui sont en lien avec le processus en jeu et comme grain le mécanisme nécessaire et suffisant pour comprendre le pattern spatial. Par exemple, si le pattern spatial est basé sur l'échantillonnage de données de dégâts d'un insecte sur une plante, la zone d'observation comprendra l'ensemble des stades de l'insecte et le grain le processus d'infestation de la plante par l'insecte. Si le pattern est basé sur l'utilisation de l'espace par les individus, la zone d'observation comprendra uniquement les stades mobiles de l'organisme considéré, et le grain le mouvement. Trouver le meilleur niveau de résolution est un problème fondamental en écologie (Grimm et al. 2005), l'effort d'échantillonnage sur le terrain comme l'effort de représentation du phénomène par des modèles mécanistes étant proportionnel à la résolution spatiale choisie. Une grande résolution organisationnelle nécessitera la prise en compte d'un grand nombre de mécanismes, complexifiant la formalisation des phénomènes en jeu et rendant le modèle peu transparent. Il s'agit donc de trouver le niveau de complexité du modèle nécessaire et suffisant pour apporter la réponse à la question posée.

Le mouvement et la dispersion des organismes sont des processus majeurs sous-tendant les patterns spatiaux. La compréhension de ces processus nécessite l'observation détaillée des mouvements individuels (Patterson et al. 2008), et les récentes avancées technologiques dans ce domaine, et en particulier l'utilisation de la radiotélémétrie (Ranius 2006), offrent de nouvelles perspectives pour quantifier la distribution précise des populations interagissant dans l'espace et dans le temps. L'analyse des données collectées varie selon

¹ On privilégiera l'anglicisme *pattern* plutôt que *patron* étant donné son usage courant dans les communautés scientifiques francophones.

qu'elles proviennent de suivis individuels répétés dans le temps ou de capture-marquage-recapture. Les données de suivi individuel considèrent les positions indexées dans le temps de chaque individu. Les trajectoires de déplacement se déduisent des positions indexées en considérant en première approximation que le déplacement entre chaque position est linéaire. Les statistiques de mouvement incluent taille de chaque segment de trajectoire, vitesse, direction absolue des trajectoires et angles de déviation entre deux segments de trajectoire (Patterson et al. 2008) (**Figure I-1a**). Les données de capture-marquage-recapture considèrent la densité d'individus présents à une certaine distance du point de lâcher. La relation entre densité et point de lâcher apporte des informations sur les paramètres moyens de dispersion, comme la distance moyenne parcourue par pas de temps (Begon et al. 1996) (**Figure I-1b**).

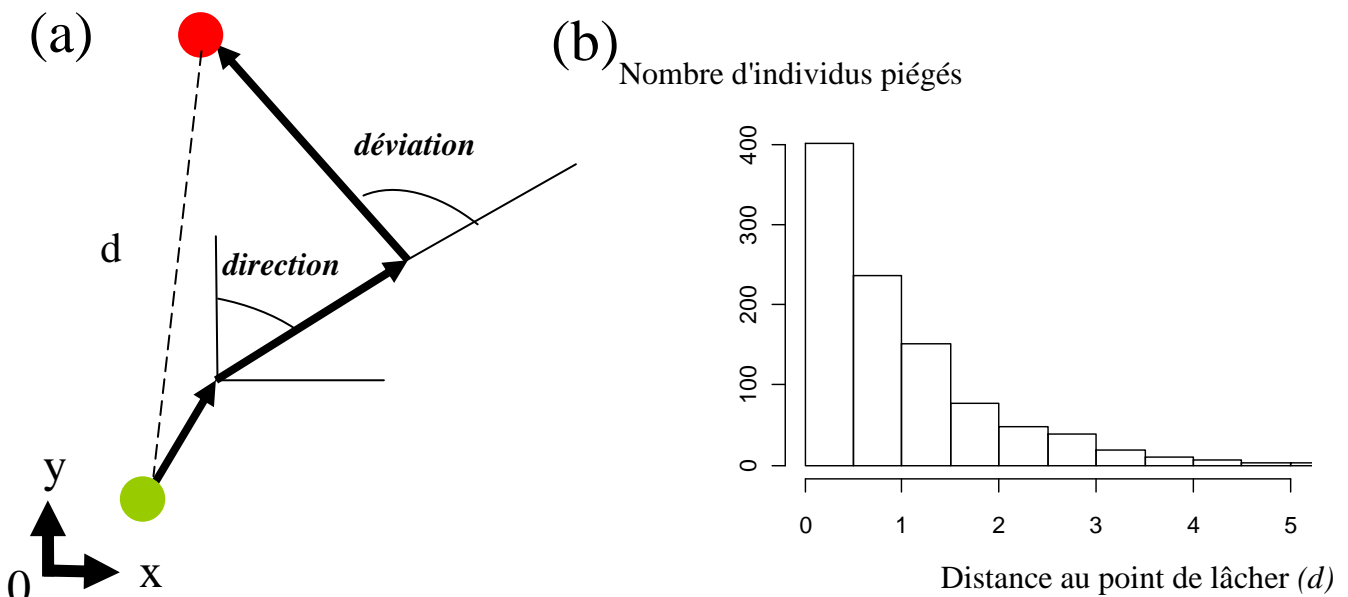


Figure I-1. (a) Schéma d'une trajectoire individuelle et (b) distribution d'un indice spatial populationnel.

Il est nécessaire de choisir le formalisme mathématique en adéquation avec les données récoltées afin de prédire la propagation et la redistribution des individus dans un environnement hétérogène. Les modèles *diffusifs* sont des outils robustes pouvant s'appliquer facilement aux données de capture-marquage-recapture et s'adapter à des modèles logistiques de croissance des populations. Au niveau individuel, les modèles de type *random walk* considèrent chaque action du mouvement (rester ou changer de lieu, quelle direction prendre, etc.) comme une combinaison d'éléments stochastiques et déterministes. Par exemple, le fait de stopper sur un habitat peut être modélisé comme un processus probabiliste, avec une probabilité de stopper dépendante de la quantité de ressources de l'habitat. Il est possible de considérer que la direction de chaque segment de trajectoire est conditionnée par la direction du segment précédent (*correlated random walk*) ou que la taille de chaque segment peut varier aléatoirement, selon une loi puissance (*Levy walk*). Les paramètres de chaque modèle peuvent être estimés par la technique éprouvée du maximum de vraisemblance (Patterson et

al. 2008) sur l'ensemble des données récoltées au champ. Les modèles ainsi définis deviennent des outils de prédiction de la distribution de l'espèce considérée, et peuvent être associés à des modèles mécanistes plus complexes, tenant compte de l'ensemble des traits de vie de l'espèce.

Dans le cadre des modèles mécanistes de dynamique spatio-temporelle, le fait de considérer l'espace de façon continue ou discrète conduit aux modèles de réaction-diffusion ou aux modèles en sites (Modèles agrégés décrits dans le **Tableau I-1**). Dans les modèles en sites, l'espace est considéré soit implicitement dans les modèles d'occupation de sites ou explicitement dans les modèles en grilles. L'approche implicite a l'avantage de se formaliser de manière synthétique. Le modèle spatialement explicite est mieux adapté pour décrire les processus locaux. L'hypothèse que chaque site interagit de manière équivalente avec tous les autres sites permet d'utiliser une nouvelle variable, la proportion de sites occupés par une espèce donnée (Caswell and Etter 1993). Cela simplifie beaucoup les expressions et l'étude analytique des conditions de coexistence des espèces. Le principal modèle d'occupation de sites pouvant être appliqué à une seule espèce est le modèle de métapopulation de Levins (Tilman and Kareiva 1997). Ce modèle est simple à résoudre analytiquement, car il fait une approximation majeure sur la dispersion. En effet, l'ensemble des sites pouvant être colonisé de manière équiprobable, ce modèle élimine l'effet d'une dispersion locale. Un cas de modèle en grille est le modèle de type "Coupled Map Lattice" (Czàran 1998), tel qu'utilisé par Lopes et al. (2010), où l'espace est constitué de nœuds discrets auxquels sont associées des équations différentielles décrivant la dynamique de ravageurs (pucerons) sur leur plante-hôte. Les plants sont couplés entre eux par des termes de migration, représentant la dispersion des individus par le vol ou la marche.

Tableau I-1 – Comparaison des différents types de modèle de dynamique spatio-temporelle de population

Modèle	Entité élémentaire	Résolution temporelle	Espace	Résolution spatiale
Modèles agrégés				
Modèle de réaction-diffusion	population	continu (équation différentielle)	explicite	continu (équation différentielle)
Modèle logistique multisite	population	continu (équation différentielle)	implicite	discontinu (composante de migration)
Modèle de Leslie multisite	population	discontinu (probabilité de passage)	implicite	discontinu (composante de migration)
Modèles en patches				
Modèle de métapopulation	patch	continu (équation différentielle)	implicite	discontinu (sites occupés/inoccupés)
"Coupled Map Lattice"	patch	continu (équation différentielle)	explicite	discontinu (discrétisation en nœuds)
Modèle automate cellulaire	patch	discontinu (pas de temps)	explicite	discontinu (discrétisation en grille)
Modèles individuels				
Modèle individu-centré	individu	généralement discontinu	explicite	discontinu (discrétisation en grille)
Modèle multi-agent	individu	généralement discontinu	explicite	discontinu (discrétisation en grille)

Le niveau de discrétisation de la population considérée peut également varier dans les modèles mécanistes (Entité élémentaire dans le **Tableau I-1**). Dans les modèles de Leslie multisite, par exemple, la population est divisée en groupes d'individus affectés par un même

processus (mortalité, mobilité, ou fécondité). Dans les modèles dit individu-centrés, par opposition aux modèles dit agrégés évoqués précédemment, où chaque individu de la population ou du groupe est identique, l'individu est pris comme grain. Les modèles agrégés de dynamique des populations sont suffisamment généraux pour s'appliquer en première approximation à de nombreuses situations. Les modèles individu-centrés portent sur le comportement des individus, et permettent de considérer explicitement la variabilité individuelle des comportements (**Figure I-2**). Les individus sont considérés comme les briques d'une population. Les interactions entre individus (micro-situation) peuvent avoir pour résultat de faire émerger certaines propriétés se situant à l'échelle de la population (macro-situation), suivant le principe d'émergence tel que défini par Grimm and Railsback (2005): *une propriété ou un comportement particulier du système est considéré comme émergent s'il n'est pas directement spécifié par les traits de l'individu*.

Le **modèle individu-centré** ou IBM (Individual-Based Model), tel qu'exposé par Ferber (1995) est un système composé des éléments suivants:

- un environnement, c'est-à-dire une représentation spatialement explicite de l'espace disposant généralement d'une métrique;
- un ensemble d'objets passifs, qui peuvent être perçus, créés, détruits et modifiés par les agents;
- un ensemble d'agents, qui représentent les entités actives du système;
- un ensemble de relations qui unissent les objets entre eux;
- un ensemble d'opérations permettant aux agents de percevoir, produire, consommer, transformer et manipuler des objets;
- des opérateurs chargés de représenter l'application de ces opérations et la réaction du monde à cette tentative de modification, appelée "loi de l'univers".

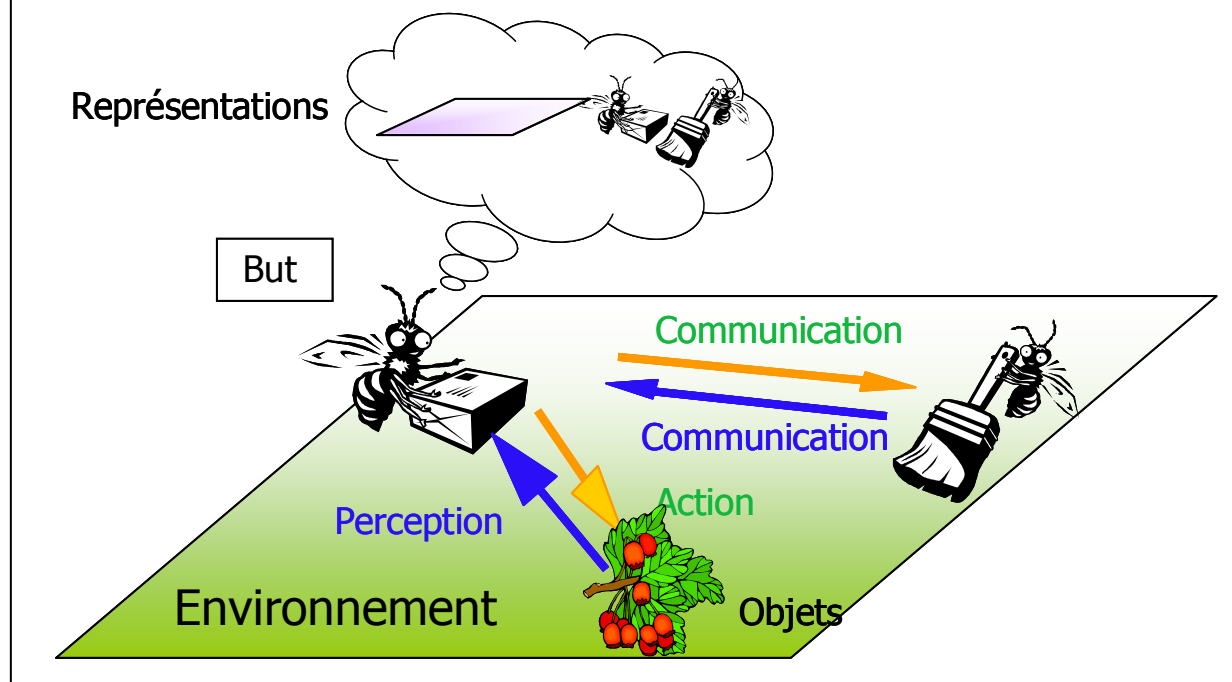


Figure I-2. Encadré expliquant le principe du modèle individu-centré d'après Ferber (1995).

2. L'organisme d'étude: le charançon noir du bananier *Cosmopolites sordidus*

Cosmopolites sordidus est originaire du Sud-Est asiatique, probablement de Malaisie et d'Indonésie, Java et Bornéo (Treverrow 1985). Cette aire d'origine est similaire à celle du bananier (Stover and Simmonds 1987). Il a ensuite progressivement envahi les plantations des différentes contrées tropicales. Sa colonisation à travers le monde aurait eu lieu principalement entre 1836 et 1906, période des plus grands transports de souches de bananiers à partir des Indes Néerlandaises, de Malaisie et d'Indochine, en direction des pays dans lesquels l'industrie bananière s'implantait petit à petit, notamment l'Afrique et l'Amérique tropicales (Cuillé and Vilardebo 1963). Sa présence est rapportée dans les zones tropicales et sub-tropicales que ce soit en Amérique, en Afrique, en Australie, en Asie ou en Océanie (Cuillé 1950; Treverrow 1985). *C. sordidus* a été observé dans les îles du Pacifique dès 1912 par Knowles and Jepson (Cuillé 1950) et dans les Antilles Françaises dès 1929 par Hustache (1929).

2.1. Caractéristiques générales et écologie

2.1.1. L'adulte

Morphologie, fécondité et longévité. L'adulte mesure de 9 à 16 mm de long (**Figure I-3**). Sa cuticule est très dure et son rostre allongé. La durée de vie de certains spécimens excède 2 ans (Froggatt 1925). La longévité moyenne au champ est estimée de 1 à 2 ans (Froggatt 1925; Vilardebo 1950). Le sexe ratio observé sur le terrain à partir de collectes est de 1 :1 en Guinée (Cuillé 1950), au Kenya (Nahif et al. 1994) et aux îles Canaries (Carnero et al. 2002). Les femelles sont généralement plus grosses que les mâles (Mestre 1995). Le rostre est plus brillant et rouge chez les femelles que chez les mâles ; il porte en outre des ponctuations à la base qui n'atteignent pas son milieu alors qu'elles l'atteignent ou le dépassent chez le mâle (Longoria 1968). La distinction des sexes d'après les microdépressions qui ponctuent le rostre est possible à l'aide d'une loupe binoculaire. La première ponte des femelles s'effectue à 33-36 jours (Cuillé 1950). La production d'œufs des femelles est faible, avec un taux estimé à 1-4 œufs/semaine (Aranzazu et al. 2000; Aranzazu et al. 2001; Arleu and Neto 1984; Cuillé 1950; Cuillé and Vilardebo 1963; Delattre 1980; Gordon and Ordish 1966; Haarer 1964; Pulido 1983; Treverrow et al. 1992; Treverrow and Bedding 1993; Vilardebo 1960, 1984). Les femelles peuvent également passer de longues périodes sans oviposition et ont la capacité de réabsorber des œufs lorsque les conditions sont défavorables (Gold et al. 2001).



Figure I-3. Adulte de charançon

Le charançon du bananier présente un cycle de vie de type 'K' (MacArthur 1962; Pianka 1970), avec une longue durée de vie et une faible fécondité, en comparaison avec d'autres espèces d'insectes ravageurs, comme les pucerons, qui sont plutôt de type 'r'.

Milieu et mode de vie. L'espèce *C. sordidus* s'alimente principalement sur les souches sauvages et cultivées du genre *Musa* (banane, plantain, abaca) (Gold et al. 2001) (**Figure I-4**). Le bananier est une plante considérée comme semi-pérenne et caractérisée par l'émission successive de rejets végétatifs. L'émission des rejets étant variable dans le temps, le développement de la population de bananier se désynchronise au cours des cycles culturaux (Tixier et al. 2004) (**Figure I-5**). Les adultes présentent une grande résistance au jeûne lorsque les conditions ambiantes limitent leur activité générale. L'insecte présente un phototropisme négatif, un hygrotropisme et un thigmotactisme² positifs (Delattre 1980; Jardine 1924; Treverrow and Bedding 1993). Au laboratoire, *C. sordidus* témoigne d'une faible résistance en atmosphère sèche : il meurt au bout de 12 heures à une humidité relative de 40% (Lemaire 1996). A l'inverse, il résiste très bien à l'immersion et peut survivre une semaine dans un bac rempli d'eau (Cuillé 1950). Son preferendum thermique est de 25°C. En période de repos, il s'accroche au matériau sur lequel il repose et s'immobilise quand il subit une pression dorso-ventrale. Par contre, en période d'activité, cette même pression déclenche une activité locomotrice. Ces réactions thigmotactiques seraient responsables du choix du milieu dans lequel l'insecte séjourne.

L'insecte a un mode de vie nocturne et essentiellement fouisseur, ce dernier comportement pouvant s'expliquer par son hygrophilie et son thigmotactisme (Cuillé and Vilardebo 1963). Les individus suivent un rythme d'activité nycthéméral comprenant environ 12 heures de repos diurne. Les individus se déplacent en marchant principalement pendant la première moitié de la nuit, l'activité des deux sexes étant légèrement décalée dans le temps (Lemaire 1996).

Les adultes sont principalement retrouvés dans les résidus de culture et les environnements humides, comme les troncs coupés ou en décomposition, les bulbes coupés ou abîmés, ou cachés sous le sol (Pavis 1988; Treverrow et al. 1992; Vilardebo 1960, 1973). Moznette (1920), Vilardebo (1960) et Treverrow et al. (1992) indiquent que les adultes sont en majorité associés aux troncs de bananiers, principalement dans les gaines des feuilles, autour des racines, sous les fibres à la base des plantes et occasionnellement dans les galeries larvaires. D'autre part, les adultes sont parfois retrouvés dans des zones ombragées et humides sous des arbustes durant le jour (Silva and Fancelli 1998).

² ou stérotactisme qui contribue à l'immobilisation des individus au contact de certains substrats.

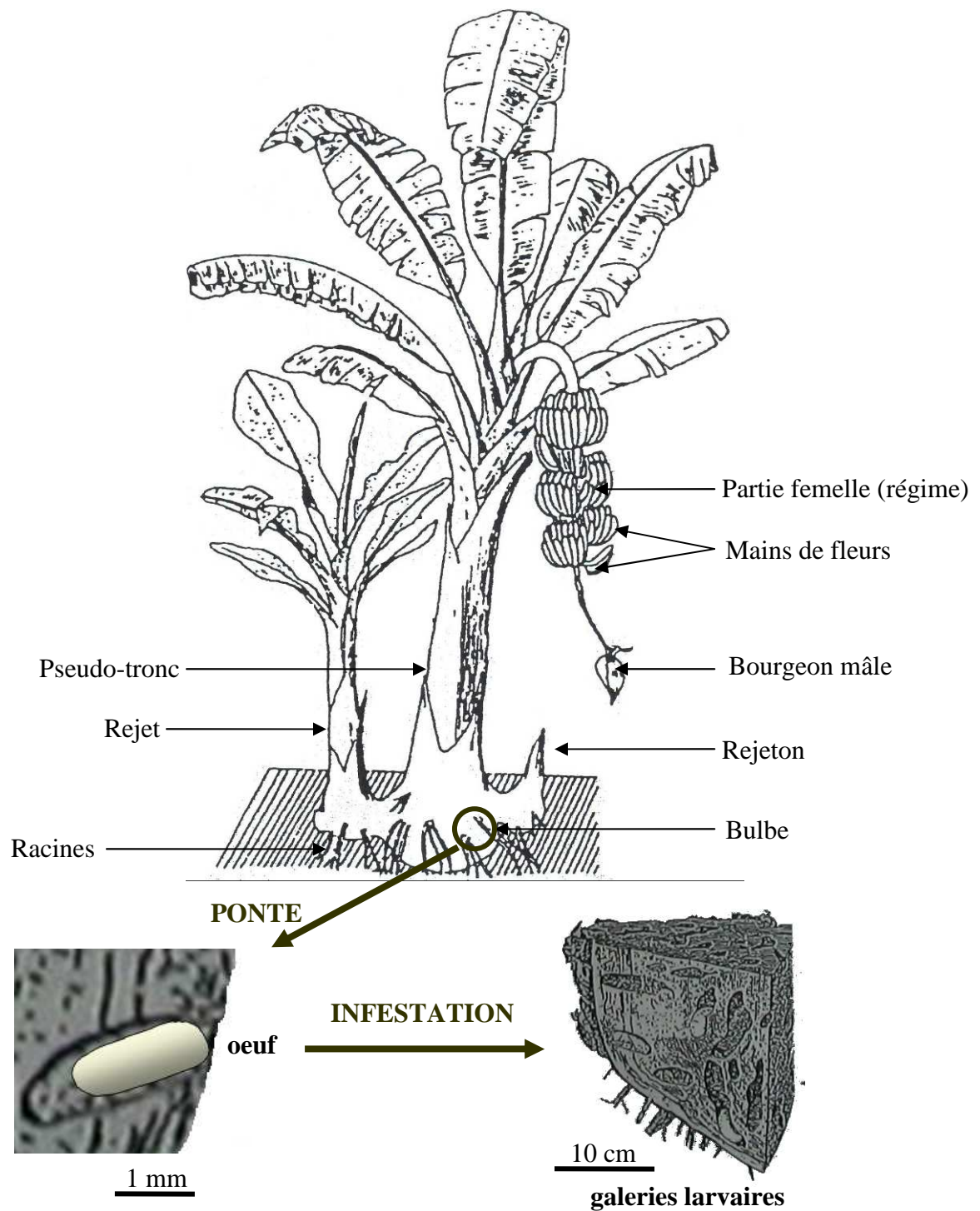


Figure I-4. Anatomie du bananier et localisation des pontes et galeries larvaires de *C. sordidus*. D'après Champion (1963), Moznette (1920) et Treverrow (1985).

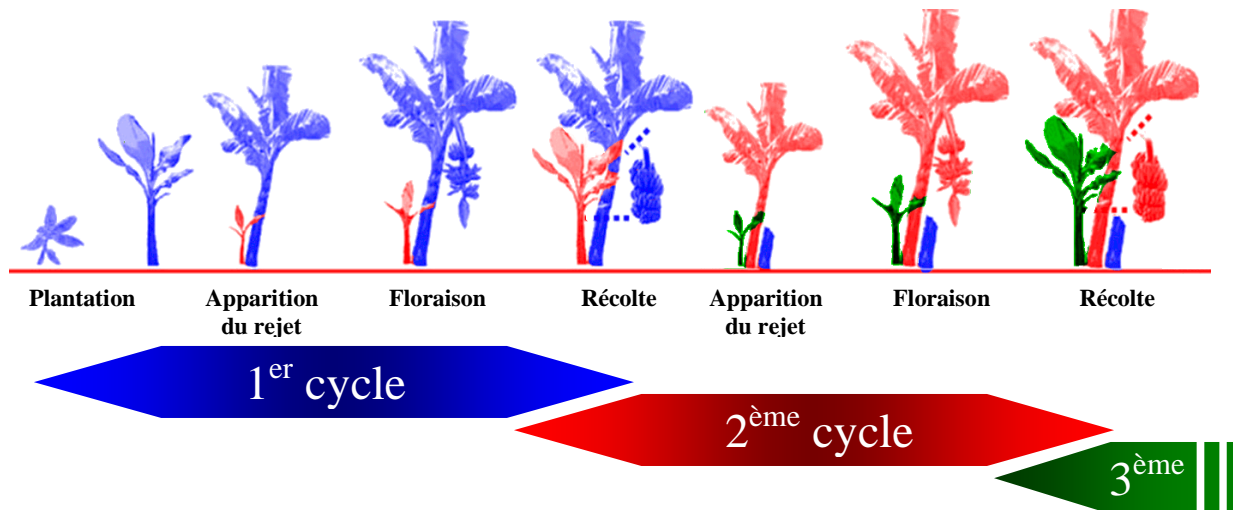


Figure I-5. Succession dans le temps des différents stades de développement du bananier. D'après Tixier et al. (2004).

Dispersion. Bien que l'adulte dispose d'ailes fonctionnelles, il n'a jamais été observé en vol (Froggatt 1925; Gordon and Ordish 1966; Greathead 1986; Nonveiller 1965; Pinese and Piper 1994; Sponagel et al. 1995; Waterhouse and Norris 1987). Lorsqu'il est soumis à des conditions extrêmes où il ne peut s'extraire que par le vol, il préfère la marche, jusqu'à ce que mort s'ensuive (Lemaire 1996). La dispersion de l'insecte se fait donc principalement par la marche, et semble limitée et lente, de l'ordre de quelques mètres par nuit et avec une tendance à rester à proximité de leur site d'émergence (Delattre 1980; Moznette 1920; Wallace 1938; Whalley 1957). Ces résultats sont à nuancer car les distances de déplacement ont été estimées par marquage-capture-recapture, où la probabilité de recapture décline en fonction de la distance au point de relâchement.

2.1.2. Les stades préimaginaux

Œuf. Les œufs sont de forme ovale allongée, d'environ 2 mm de long et d'un blanc franc (Treverrow 1985) (Figure I-6). Ils sont déposés séparément sur les plantes-hôtes dans des petites cavités creusées par la femelle à l'aide de son rostre. L'oviposition est généralement pratiquée à la base des plantes, au niveau du sol (Gold et al. 2001) et est très peu fréquente sur les racines (Abera-Kalibata 1997). Les œufs, placés au-dessus ou en dessous de la surface du sol, présentent ou non une vulnérabilité aux ennemis naturels (Koppenhofer 1993a). La durée d'incubation des œufs varie généralement de 4 à 7 jours, en fonction des conditions climatiques, et la durée moyenne a été estimée à 6.9 jours par Viswanath (1976).



Figure I-6. Œuf de charançon

Larve. La larve mesure 10 à 12 mm de long à la fin de sa croissance, immédiatement avant la nymphose. Elle est apode et son corps, faiblement recourbé, se dilate progressivement à partir de l'abdomen jusqu'aux segments V et VI puis se rétrécit à partir de ce niveau, ce qui donne à la larve un aspect ventru différent des larves classiques de *Curculionidae* (**Figure I-7**). Elle est de couleur blanc crème avec une tête brun-rouge foncé et volumineuse, armée de fortes mandibules (Moznette 1920; Treverrow 1985). La morphologie des larves n'est pas fondamentalement différente d'un stade à l'autre (Cuillé and Vilardebo 1963). Le nombre de stades est aussi variable (5 pour Cendana (1922) ; 6-7 pour Montellano (1954) et 7 pour Viswanath (1976). Il semble que la durée de chaque stade soit similaire, et par conséquent le nombre de stades augmenterait en fonction de la durée de développement larvaire. Les durées de développement larvaire et post-larvaire varient largement, de 12 à 165 jours pour les larves, de 1 à 4 jours pour les prépuces et de 4 à 30 jours pour les nymphes car elles sont température-dépendantes (Traore et al. 1996; Traore et al. 1993).



Figure I-7. Larve de charançon

La larve creuse des galeries dans la base du bulbe de bananier dont le diamètre augmente progressivement en fonction du développement de la larve. Elle est capable de consommer le double de son volume en tissus de bananier par jour. Le tracé de la galerie (jusqu'à 170 mm de long) ne débouche jamais à l'extérieur et est limité au bulbe. La grande majorité des galeries est située à la périphérie du bulbe, dans la zone corticale et légèrement en dessous de son plus grand diamètre (Vilardebo 1973). Lorsque cette zone est entièrement colonisée, les larves nouvellement écloses s'alimentent dans les autres parties du bulbe, d'abord sa partie inférieure puis le centre ; ce n'est que lorsque ce dernier est totalement miné que les larves cherchent dans le pseudo-tronc ou encore dans le jeune rejet des conditions favorables à la poursuite de leur développement. La répulsion apparente du pseudo-tronc proviendrait d'une trop forte teneur en eau de ses tissus.

Nymphe et ténéral. La nymphose s'effectue dans un cul-de-sac de la galerie, généralement situé à la périphérie de la souche. La durée de vie nymphale est de 4 à 22 jours. La nymphe est blanche et mesure 12 mm de long (Treverrow 1985) (**Figure I-8**). Les adultes émergeant des loges nymphales demeurent dans les loges à l'intérieur des plantes. La couleur des jeunes adultes est brun-rouge puis vire au noir lors du durcissement de l'exosquelette. En conditions tropicales, le stade ténéral peut durer de 2 à 14 jours (Froggatt 1925; Jardine 1924; Mestre 1997; Montellano 1954).



Figure I-8. Pupe de charançon

2.2. Dynamique d'infestation des parcelles de bananeraies

Contamination des parcelles. Lors de la replantation d'une parcelle de bananes, les rejets plantés peuvent contenir des œufs, des larves et occasionnellement des adultes. Par conséquent il y aura contamination de la parcelle par de multiples foyers (Gold et al. 2001). Afin de préserver les parcelles saines, il est nécessaire de planter du matériel biologique sain (vitroplants). Une parcelle saine peut être contaminée par une parcelle avoisinante ayant une pression très forte en charançons car des migrations d'individus surviennent le long des bordures jouxtant les parcelles contaminées. La recolonisation est en général lente et commence par des dégâts au niveau des bordures (Mestre and Risède 1997). Lorsque la parcelle est déjà infestée en charançons, une replantation sur précédent bananes entraîne des dégâts importants (Mestre and Risède 1997).

Progression de l'infestation. Du fait de la faible fécondité des femelles, l'accroissement des populations est faible et nécessite plusieurs cycles avant d'être pleinement établi (Arleu and Neto 1984). Selon Cuillé (1950), après la contamination d'une parcelle, les foyers de populations se développent et se multiplient pendant quelques mois à deux ans. A ce stade de l'infestation, les dégâts ne sont pas encore visibles car seules quelques larves sont présentes dans les bulbes. Il faut une dizaine de larves à l'intérieur d'un bulbe pour que la plante présente extérieurement des signes d'affaiblissement. Au fur et à mesure de l'accroissement des populations, les bananiers deviennent sévèrement atteints et sont souvent déracinés par les vents ou ont des régimes atrophiés. Si la plantation est particulièrement délaissée, la pullulation peut devenir d'une importance considérable ; chaque talle abrite un nombre suffisant de charançons pour attaquer systématiquement chaque nouveau rejet, peu nombreux sont les pieds arrivant à maturité ; ils sont alors atteints de nanisme et porteurs d'un régime minuscule à une ou deux mains atrophiées.

Niveaux de populations. Les densités de charançons dans les bananeraies ont été estimées par des techniques de capture-marquage-recapture. Delattre (1980) a estimé ces densités dans 2 parcelles différentes à respectivement 2600 individus/ha et 15 600 individus/ha, ce qui représente des densités de 10 à 337 adultes par pied. En Ouganda, les densités ont été estimées entre 6 et 17 individus/pied (Gold et al. 2001). Du fait des faibles capacités de dispersion de l'insecte, la distribution spatiale des populations est agrégée à de multiples foyers (**Figure I-9**). Il n'existe pas d'informations à ce jour sur l'influence du climat sur les niveaux de population. Les populations étant estimées par piégeage, il est difficile de distinguer l'effet de l'efficacité du piégeage de celui de l'accroissement de la population.

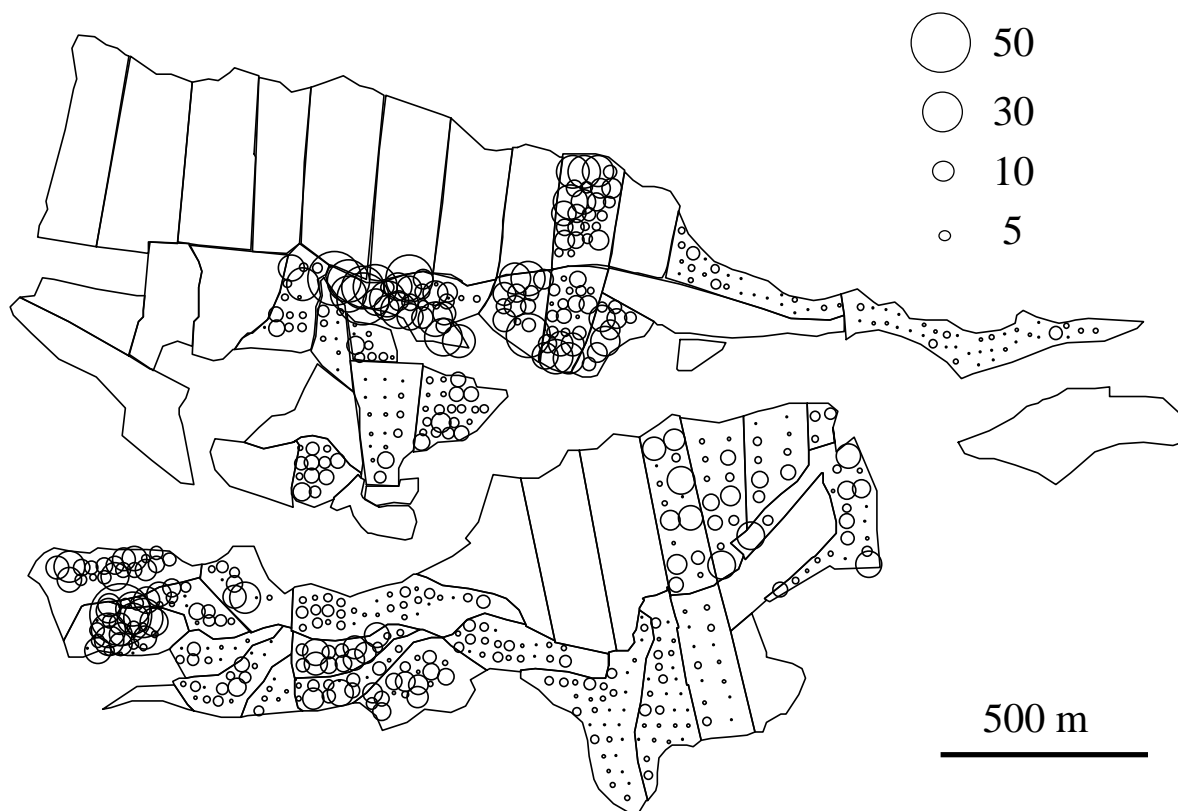


Figure I-9. Cartographie de niveaux de populations de *C. sordidus* estimés à partir d'un maillage régulier de pièges à phéromone dans un ensemble de parcelles, indiquant l'hétérogénéité spatiale des populations. La taille du cercle représente le nombre d'individus par piège.

Nuisibilité. L'essentiel des dégâts causés par *C. sordidus* sur bananier est dû aux larves. Ces dernières, en creusant des galeries pour s'alimenter à l'intérieur des bulbes de bananier, sont responsables de la rupture des tissus du bulbe qui sont constitués de fibres et de canaux vasculaires. Elles perturbent ainsi les communications entre la racine et les autres organes. De ce fait, un grand nombre de racines sont détruites. Les plants infestés sont plus fragiles et un grand nombre de bananiers peuvent être déracinés par le vent, ce qui est la première cause de dégâts de *C. sordidus* aux Antilles. Les dégâts vont s'accumuler au fur et à mesure des cycles culturaux, en fonction de l'accroissement de la population de l'insecte. Il a également été constaté un certain nanisme des bananiers adultes et la présence de régimes de petite taille et mal formés (Lemaire 1996). En outre, ces galeries représentent une porte d'entrée à des agents pathogènes secondaires tels que *Ralstonia solanacearum* et *Fusarium oxysporum* (Castrillon 1991) provoquant un pourrissement du bulbe. Une étude menée en plein champ entre 1994 et 2001 en Ouganda a montré des pertes de récolte de 47% après 4 ans d'essai, dues à des diminutions du poids des régimes, à un moins grand nombre de régime ainsi qu'à des pertes de bananiers (Gold et al. 2004). Une autre étude confirme ces résultats, en rapportant des pertes de récolte de 5% pour le premier cycle et atteignent 44% au 4^{ème} cycle, principalement attribuées à la perte de poids des régimes (Rukazambuga et al. 1998).

2.3. Stratégies de lutte contre le charançon du bananier

Jusqu'aux années 90, la principale technique de lutte contre le charançon était chimique. Le chlordécone, pesticide organochloré, a été utilisé aux Antilles Françaises (Vilardebo et al. 1974), puis a été interdit en 1993 du fait de sa toxicité et de sa forte persistance. Devant l'absence de lutte chimique efficace au chlordécone, des méthodes de lutte alternatives ont été utilisées ou sont envisagées et sont exposées ci-après.

Piégeage de masse. Lorsqu'ils ont été récemment en contact avec du pseudo-tronc et probablement après s'en être nourris, les mâles produisent une phéromone d'agrégation (sordidine) principalement pendant la nuit (Lemaire 1996). Cette substance est synthétisée et utilisée dans des pièges d'interception enterrés. Après mise en jachère, il est recommandé de placer les pièges dans les bordures de la parcelle détruite afin de limiter la contamination des parcelles avoisinantes (Rhino et al. 2010). Le rayon d'action des pièges et les facteurs influençant l'efficacité du piégeage sont encore méconnus et nécessitent des études approfondies afin d'optimiser la disposition spatiale des pièges à l'échelle de la parcelle, voire du réseau de parcelles.

Rotation culturale et prophylaxie. La mise en jachère des parcelles pendant plusieurs mois permet de priver l'insecte de ses ressources, d'où une diminution des populations due à la perte des lieux de ponte et l'émigration des individus vers des parcelles plantées avoisinantes (Gold et al. 2001). L'organisation spatiale de la mise en jachère doit être traitée à l'échelle du réseau de parcelles afin de limiter les recontaminations. Suite à la mise en jachère, l'utilisation de plants sains (vitroplants) lors de la replantation permet de limiter l'infestation initiale des bananeraies et retarde l'accroissement de la population pendant plusieurs cycles culturels (Lassoudière 2007). Lors de la replantation, l'organisation spatiale des pieds de bananiers pourrait influencer la dynamique d'infestation du charançon et doit être analysée en conséquence comme potentiel levier d'action.

Variétés de bananier plus ou moins résistantes au charançon. Il semble que les niveaux de dégâts provoqués par les attaques de charançons soient influencés par les variétés de bananiers, sélectionnées ou non (Kiggundu et al. 2003). Cette résistance du bananier à *C. sordidus* peut intervenir lors de la recherche de l'hôte par le ravageur, lors de la ponte ou pendant le développement larvaire. Il semble que les variétés sensibles et résistantes se sont avérées d'une attractivité comparable au laboratoire (Lemaire 1996), mais il est nécessaire de confirmer ces résultats au champ. Le choix de ponte s'est révélé également comparable quelle que soit la variété (Kiggundu et al. 2007), le phénomène d'antibiose se manifestant uniquement lors de la dernière étape avec une mortalité importante des larves et un développement ralenti sur les variétés résistantes (Kiggundu et al. 2007; Lemaire 1996).

Aménagement de l'habitat. La gestion des cultures joue un rôle important dans la régulation des populations de charançons. Les fortes pressions d'infestation ont souvent été associées à de faibles niveaux de gestion des cultures, des plantes stressées, un mauvais drainage, des sols acides ou avec une faible fertilité, un mauvais état sanitaire, une sécheresse prolongée et une forte infestation de nématodes (Bakyalire 1992; Froggatt 1925; Treverrow et al. 1992; Veitch 1929; Wallace 1938). Les résidus de culture pouvant servir d'abris pour les adultes (Gold et al. 1999b), la limitation des quantités de résidus dans les parcelles permettrait un contrôle des populations. L'effet de la réorganisation des résidus de culture sur la dynamique spatiale du charançon est encore méconnu. Leur utilisation comme levier d'action pour limiter la dynamique du bioagresseur est à envisager.

3. Bases et objectifs de la thèse

L'organisation spatiale du système de culture est un élément clé à prendre en compte dans la lutte contre *C. sordidus*. Le charançon du bananier est un insecte marcheur dont les mouvements sont fortement influencés par les éléments de l'agroécosystème. A l'échelle de la parcelle, son environnement est constitué de sol nu, pieds de bananiers, résidus de culture et pièges à phéromones. A l'échelle du réseau de parcelle, les parcelles sont séparées par des routes, bordures enherbées ou ravines. A l'heure actuelle, les principales stratégies de lutte contre le charançon qui sont recommandées aux planteurs portent sur l'utilisation de pièges à phéromones et la mise en jachère des parcelles cultivées.

Or très peu de connaissances existent sur la dynamique spatiale du charançon, et en particulier sur les mécanismes d'interaction des individus avec leur environnement. Ces connaissances sont fondamentales pour optimiser les stratégies de lutte déjà existantes et en définir de nouvelles basées sur l'organisation spatiale des plantations et des résidus de culture. L'objectif général de cette thèse est d'étudier les relations entre la dynamique spatiale du ravageur et l'hétérogénéité spatiale des ressources. Il s'agit d'une part de quantifier et de comprendre, en combinant expérimentation et modélisation, les processus sous-tendant la dynamique spatiale des populations afin de s'en servir comme leviers dans le contrôle du bioagresseur. L'objectif général se décline en quatre objectifs particuliers:

1. **quantifier le mouvement du charançon adulte afin de tester s'il est influencé par la configuration parcellaire;**
2. **analyser et représenter le mouvement du charançon pour l'intégrer dans un modèle mécaniste afin de tester si sa perception de l'espace est variable suivant son habitat de résidence;**
3. **intégrer dans un modèle les autres processus démographiques affectant la distribution des attaques de charançons afin d'en étudier l'importance relative;**
4. **proposer à partir du modèle des configurations spatiales de plantation et d'organisation des pièges limitant les populations de charançons.**

La démarche générale de **compréhension des processus** est basée sur la comparaison de patterns issus de données récoltées sur le terrain avec des données simulées par un modèle mécaniste. Cette approche est discutée dans le Chapitre II, ainsi que l'intérêt de combiner les statistiques de données spatialisées et la modélisation mécaniste dans une démarche de compréhension d'un pattern spatial. Le premier objectif de l'étude a nécessité la mise au point d'une méthode originale permettant de suivre des insectes marcheurs au comportement cryptique se déplaçant dans un habitat hétérogène (1^{er} objectif, Chapitre III). Nous avons appliqué une méthode de suivi par télémétrie en marquant individuellement les adultes avec des puces RFID (Radio Frequency Identification) passives. La multiple recapture des individus dans le temps a permis de représenter leurs trajectoires de déplacement. Les patterns issus de données spatialisées ont été caractérisés par des statistiques circulaires. L'effet des facteurs environnementaux sur les déplacements a été étudié, en particulier la disposition spatiale des éléments des parcelles (**Figure I-10**).

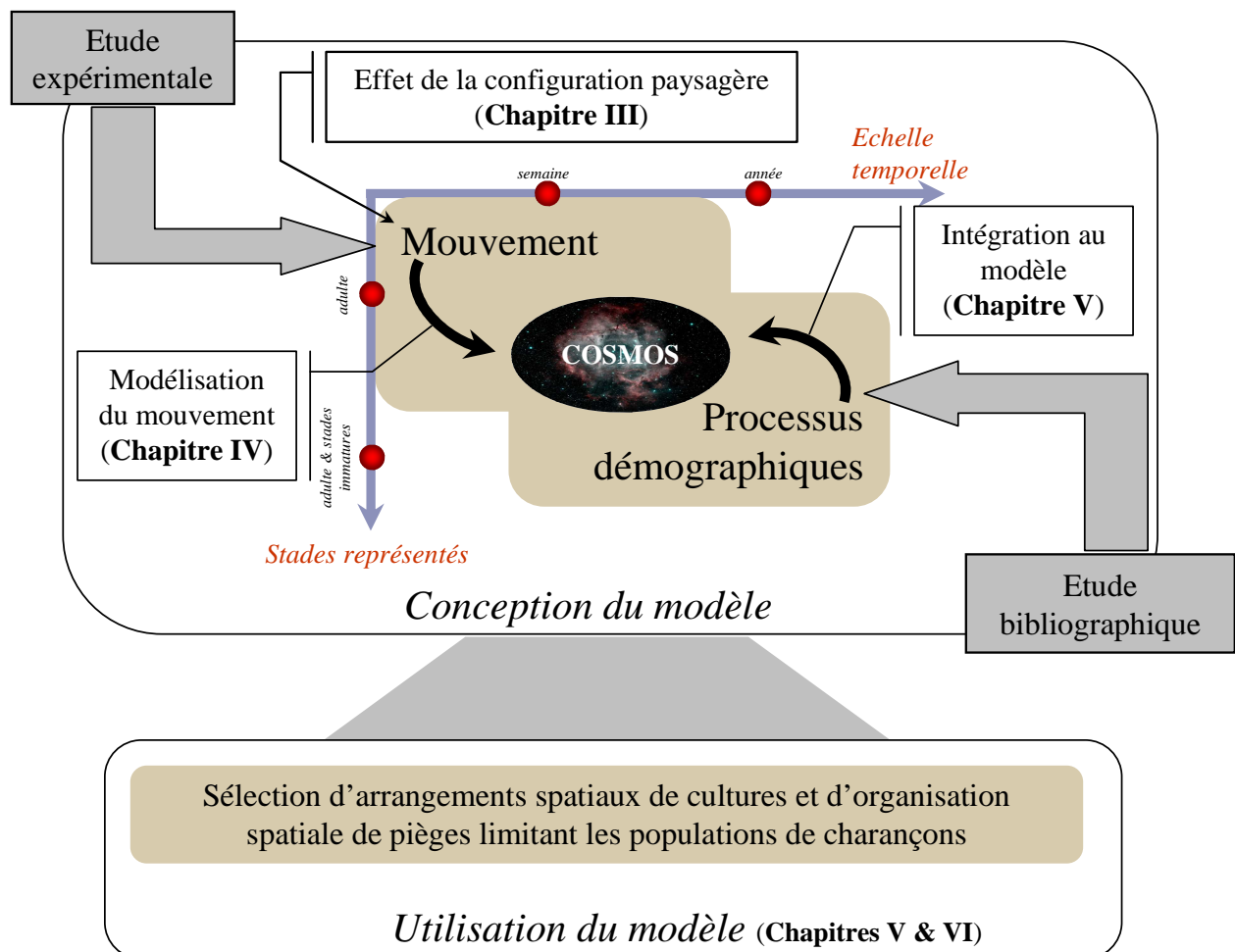


Figure I-10. Schéma synthétique représentant l'articulation des objectifs dans la thèse.

Dans le Chapitre IV (2^{ème} objectif), le mouvement individuel a été considéré comme une succession de déplacements dans une grille. Les pièges à phéromone, éléments d'habitat particuliers, n'ont pas été considérés dans ce chapitre. Chaque déplacement tient compte du potentiel de préférence de l'habitat de destination et d'une perception de l'espace³ dépendante de l'habitat de départ, estimés par maximum de vraisemblance. La décomposition du mouvement la plus pertinente a été choisie en fonction de son adéquation avec les patterns réels, suivant la démarche définie par Grimm et al. (2005). Ce processus a été intégré dans un modèle stochastique et individu-centré (Figure I-10). Le choix de ce type de modèle est motivé par l'importance des comportements individuels et des relations avec l'environnement local dans la dynamique des populations de charançons.

Ce modèle stochastique, nommé COSMOS par la suite, a été complété par des processus démographiques afin de simuler l'infestation des parcelles. Les processus considérés comme importants dans la compréhension des patterns d'infestation des bananeraies ont été intégrés au modèle grâce aux données bibliographiques existantes (**Figure I-10**). L'importance des processus intégrés a été discutée au regard de l'analyse de la sensibilité des paramètres du modèle (3^{ème} objectif, Chapitre V).

Afin de replacer les objectifs de la thèse dans le cadre appliqué de la lutte contre les ravageurs, les propriétés émergentes du modèle ont été explorées en simulant des arrangements spatiaux de plantation et de pièges afin de sélectionner le meilleur arrangement permettant le contrôle des populations de charançons (**Figure I-10**). Le potentiel de préférence des pièges par rapport aux autres éléments du paysage a été calculé sur la base de deux essais réalisés au champ. Les arrangements de plantations et de pièges ont été caractérisés par des indices spatiaux (4^{ème} objectif, Chapitre VI).

³ ou fonction de portée, désigne une fonction mathématique décrivant la manière dont l'attractivité d'une localisation décroît en fonction de sa distance au récepteur.

CHAPITRE II - OUTILS ET METHODES POUR COMPRENDRE L'HETEROGENEITE SPATIALE DES POPULATIONS

L'hétérogénéité spatiale des populations peut être causée par des facteurs biotiques et abiotiques. Lier ces facteurs aux patterns spatiaux est primordial pour mieux comprendre et prédire les dynamiques d'insectes.

Ce chapitre repose sur l'article de revue publié dans *Methods in Ecology and Evolution* et intitulé **Factors and mechanisms explaining spatial heterogeneity: A review of methods for insect populations**.

Le premier objectif est d'établir l'état des lieux de l'ensemble des outils et méthodes ayant été appliqués sur insecte, et de comparer deux approches a priori complémentaires, mais rarement utilisées conjointement: les statistiques spatiales et les modèles mécanistes.

Le deuxième objectif est de proposer une démarche générale de compréhension des processus sous-tendant les patterns spatiaux, de type itératif, où interviendront successivement les approches statistiques et mécanistes. La **Figure II-1** présente une démarche de caractérisation de patterns à partir d'indices statistiques basés sur l'échantillonnage d'une population d'insectes avec des pièges attractifs. Une fois le pattern défini, les modèles statistiques de régression permettent de sélectionner les facteurs affectant le pattern. Enfin, les modèles mécanistes peuvent être utilisés pour analyser comment les processus affectent le pattern, en simulant les patterns selon diverses hypothèses de processus et en les confrontant à la réalité.

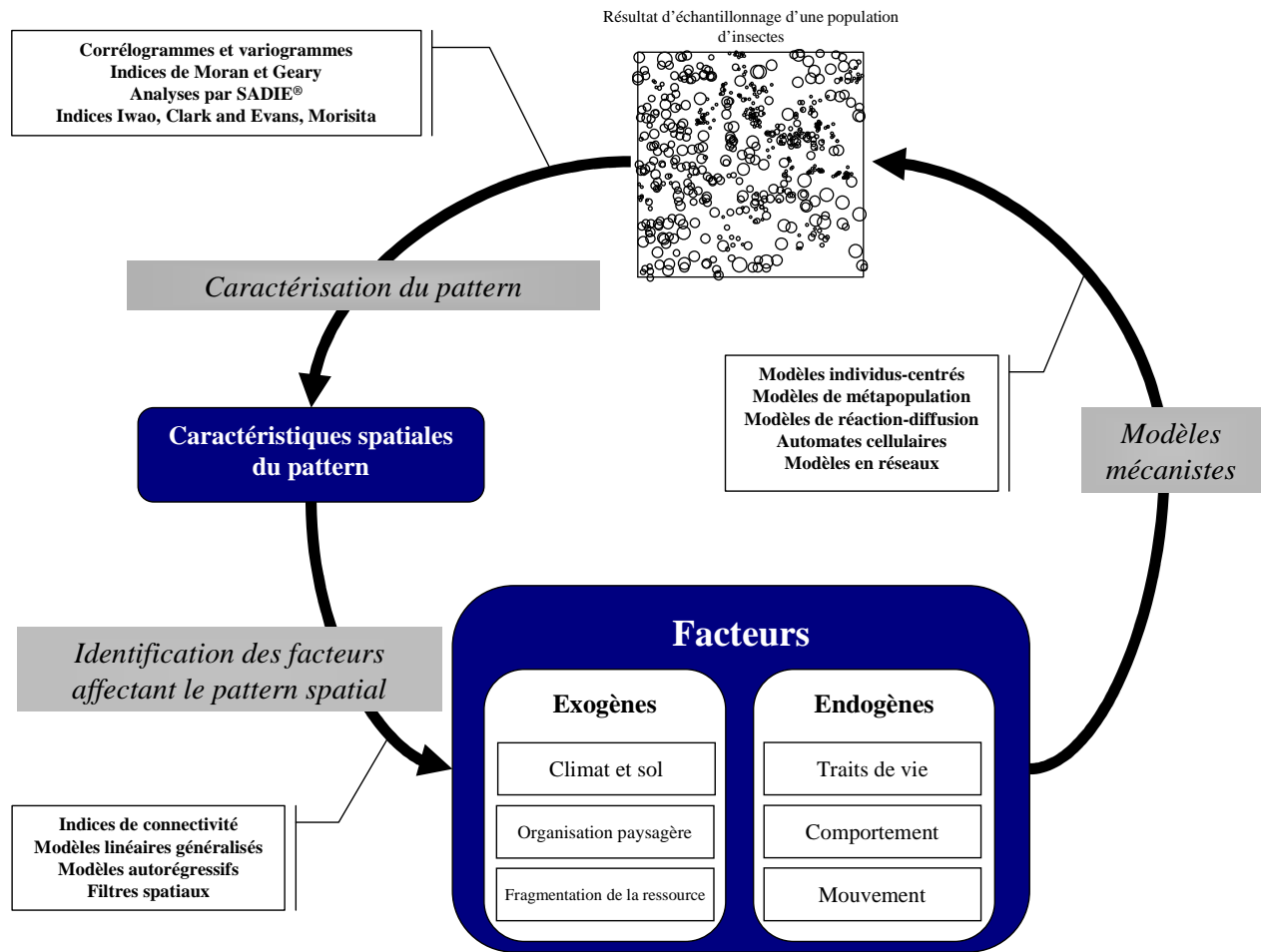


Figure II-1. Schéma général de la démarche de compréhension d'un processus affectant la distribution spatiale d'une population.

Factors and mechanisms explaining spatial heterogeneity: A review of methods for insect populations

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Abstract

- 1.** The spatial distribution of populations is affected by the dispersal abilities of the species, interactions among individuals, or habitat selection. Linking these ecological processes to spatial patterns is of primary importance for understanding and prediction purposes.
- 2.** We review both statistical and mechanistic methods for studying the spatial distribution of populations. Statistical methods, such as spatial indexes and nearest neighbour analyses help characterizing the spatial pattern. They allow testing the effect of environmental variables on spatial patterns using regression analyses.
- 3.** Mechanistic modelling can be used to analyse the effect of mechanisms underlying the spatial pattern. We review mechanistic models (e.g., metapopulation, individual-based and cellular automaton models) devoted to represent dispersal abilities, interactions among individuals and habitat selection.
- 4.** We illustrate each method by works on insects, which cover a broad range of spatial patterns. Strengths and limitations of methods are discussed according to the process and type of data set.
- 5.** Scientists can use statistical or mechanistic methods in an iterative manner to infer process from spatial pattern. New approaches such as "pattern-oriented modelling" or "space as a

surrogate framework" determine whether alternative models reproduce an observed pattern. It allows selection of the process that best explain the observed pattern.

Keywords: Spatial pattern, Spatial analysis, Mechanistic model, ecological process.

1. Introduction

Spatial heterogeneity is of great importance in the study of populations, communities, ecosystems, and landscapes (Shaver 2005). Spatial heterogeneity is defined either as the variation in space in distribution of a point pattern, or variation of a qualitative or quantitative value of a surface pattern (Dutilleul & Legendre 1993). It can be caused by habitat factors (Tscharntke *et al.* 2002) and their temporal variations (Leyequien *et al.* 2007), individual traits (Tilman & Kareiva 1997), and neutral processes (Rosindell, Wong & Etienne 2008). Habitat factors include resource density and heterogeneity that may result in a series of suitable patches of different size and of different isolation level in an unsuitable matrix (Tscharntke *et al.* 2002). When habitat is fragmented, the dispersal behaviour of individuals explains much of the variation of population densities in corresponding patches (Coombs & Rodriguez 2007). Individual traits such as dispersal abilities (Tscharntke & Brandl 2004), sexual attraction by pheromone, or aggregative behaviour have consequences for population dynamics and species distributions.

Linking ecological processes, such as dispersal, interactions among individuals, or habitat selection, to spatial patterns is of primary importance in both basic and applied ecology. It may help the conservation of endangered species (Matern *et al.* 2007) based on the comprehension of the effects of habitat fragmentation on population dynamics (McIntire, Schultz & Crone 2007), and to control pest species by relating their spatial distribution to their damages (Eber 2004; Rodeghiero & Battisti 2000).

Methods used to analyse the spatial heterogeneity of populations are statistical or mechanistic. Statistical methods based on spatial correlations or multiple regressions on landscape variables help reveal the link between landscape elements and populations. They allow the researcher to characterize spatial patterns and to test the explanatory power of candidate variables using a correlative approach. Mechanistic methods deal with underlying

mechanisms of spatial distribution of populations that are studied at the population or individual scale. The combination of statistical and mechanistic models in ecological research can provide new insights into the comprehension of spatial heterogeneity.

In this review, we argue that the comprehension of spatial heterogeneity requires an iterative process including three steps. The first part of the review presents the use of statistical methods to detect the characteristics of spatial patterns (**Figure II-2: arrow 1**). The second part of the review presents the statistical models used to identify exogenous or endogenous factors explaining a spatial pattern (**Figure II-2: arrow 2**). The third part of the review exemplifies the use of mechanistic models to study the mechanisms that produce spatial patterns. In the last part of the review, we discuss the methodological ways to link spatial patterns and ecological processes, and especially how statistical and mechanistic methods complement each other to achieve a full understanding of spatial heterogeneity of population (**Figure II-2: arrow 3**). Rather than presenting in detail methods, which has been done elsewhere for statistical methods (e.g. Cressie 1993; Dale *et al.* 2002; Fortin & Dale 2005), mechanistic methods (e.g. Huffaker & Gutierrez 1999; Tilman & Kareiva 1997), and pattern-process approach (Illian *et al.* 2008), our review aims at providing a framework for choosing the right method or the best combination of methods to explain the spatial pattern of a population. We illustrate the strengths and limitations of methods with insect case studies, because of the wide range of spatial patterns and life-history traits in insect populations (Schowalter 2006). **Table II-1** and **Table II-2** illustrate the topics of the research conducted on spatial heterogeneity of insect population during the last fifteen years by statistical or mechanistic methods, respectively. Each table allows researchers to know existing methods already used to address a given topic.

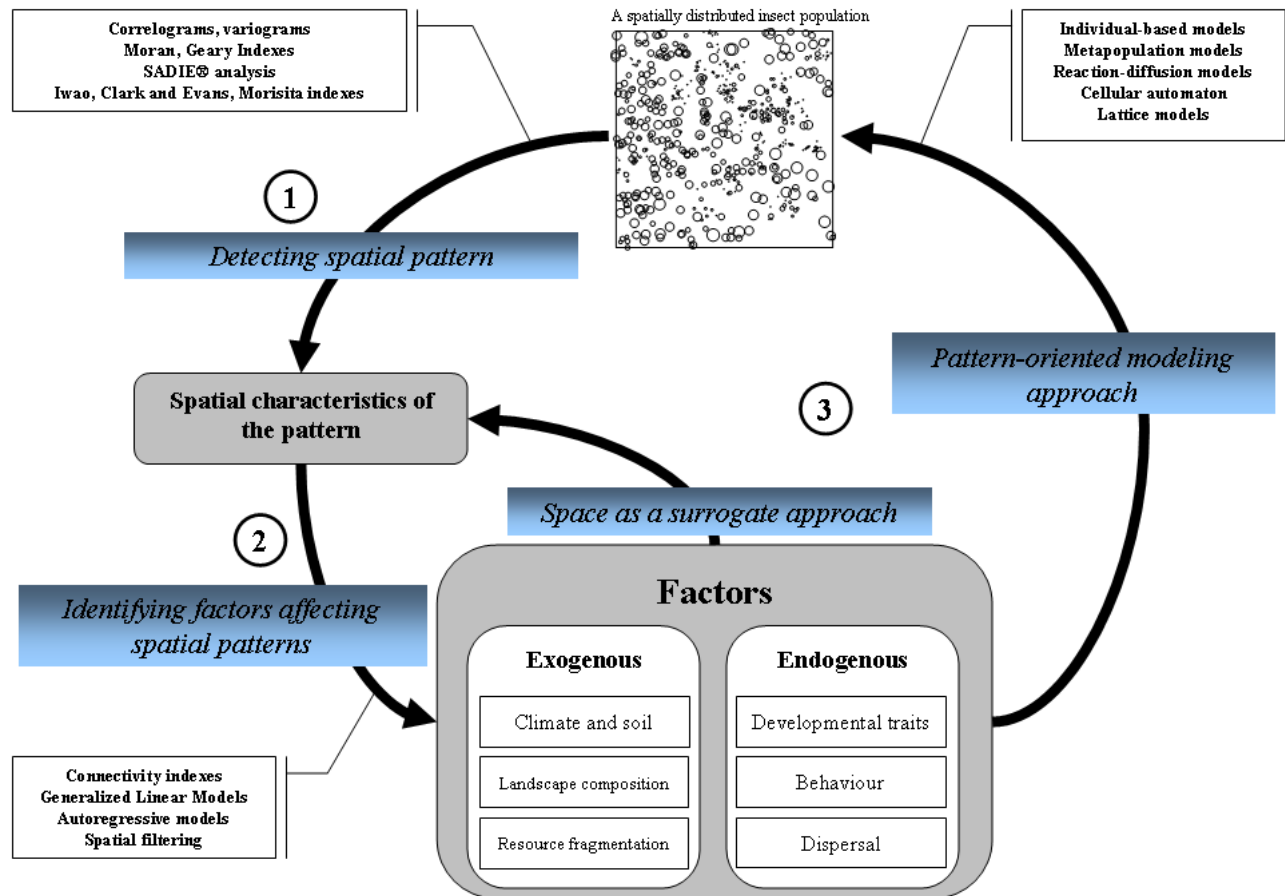


Fig II-1. Schematic diagram of the different steps necessary to understand spatial heterogeneity of organisms and the type of methods involved.

2. Characterization of the spatial pattern of insect populations

Spatial and temporal resolutions of the sampling area are of primary importance to capture the process under study and should be adapted in consequence (Fortin & Dale 2005). For example, the distribution of a population of aphids may seem to be aggregated, random, or regular depending on whether the forest, tree, or leaf is chosen as sampling unit (Begon, Harper & Townsend 1996). Geostatistical methods have to be chosen among indexes of spatial autocorrelation (e.g., Moran and Geary, SADIE®, Mantel) and analysis of neighbouring distances (e.g., Nearest-neighbour distance or K-function) (**Table II-1, Figure II-2: arrow 1**).

Table II-1. Overview of statistical models used to characterize spatial patterns of insect populations and corresponding references.

Topic	Method	References
Characterization of the spatial population pattern		
Evaluation of distribution of species	Kriging	(Franceschini, Cannavacciuolo & Burel 1997; Moral García 2006; Trematerra <i>et al.</i> 2007)
	Trend surface analysis	(Felizola Diniz-Filho & Fowler 1998)
Identification of species patterning (aggregation)	Moran Eigenvectors	(Jombart, Dray & Dufour 2009)
	SADIE®	(Ferguson <i>et al.</i> 2003; Nansen, Subramanyam & Roesli 2004; Thomas <i>et al.</i> 2001)
	Mantel test, Moran and Geary Indexes	(Ellis 2008a; Judas <i>et al.</i> 2002; Rodeghiero & Battisti 2000)
	Lloyd's index	(Kianpour <i>et al.</i>)
	Ripley's K-function, Taylor's power law	(Lancaster, Downes & Reich 2003; Powers <i>et al.</i> 1999; Schroff, Lindgren & Gillingham 2006)
	Iwao's patchiness regression	(Arnaldo & Torres 2005; Peña <i>et al.</i> 2007)
	Morisita's Index	(Gilbert <i>et al.</i> 2001)
	Clark & Evan's Index	(Chamorro-R <i>et al.</i> 2007)
	Nearest-neighbour distance	(Dodds <i>et al.</i> 2006; He & Alfaro 1997)
	Bayesian approach	(Augustin <i>et al.</i> 2007)
Egg-laying pattern	Nearest-neighbour distance	(Moravie <i>et al.</i> 2006; Potts & Willmer 1998)
	Frequency distribution fitting	(Desouhant <i>et al.</i> 1998; Zu Dohna 2006)
Identification of factors affecting spatial patterns at the landscape scale		
Landscape factors		
* Habitat unsuitability (border effects...)	Multiple regression analysis	(Den Belder <i>et al.</i> 2002; Holland & Fahrig 2000)
	Stepwise regression	(Buse, Schroder & Assmann 2007; Elliott <i>et al.</i> 1999; Matern <i>et al.</i> 2007)
* Habitat suitability	Generalised linear mixed models	(Taboada <i>et al.</i> 2006)
	Correlation with proximity indexes	(Beckler <i>et al.</i> 2004; Fred <i>et al.</i> 2006; Hanski & Heino 2003)
	ANOVA analysis	(O'Rourke, Liebman & Rice 2008)
	Autoregressive models	(Kadoya <i>et al.</i> 2009)
	Spatial-filtering	(Hamasaki <i>et al.</i> 2009)
	Generalized linear models	(Botes <i>et al.</i> 2006)

Climate factors	Autoregressive models	(Aukema <i>et al.</i> 2008)
	Spatial-filtering	(Fergnani, Sackmann & Cuzzo 2008)
	Nearest-neighbour distance	(Scharf <i>et al.</i> 2008)
Habitat fragmentation	Generalised linear mixed models	(Fred <i>et al.</i> 2006; Li <i>et al.</i> 2007; Powers <i>et al.</i> 1999; Rabasa <i>et al.</i> 2005; Tschamtké <i>et al.</i> 2002)
	* Patch indexes	Multiple regression analysis
		(Krauss, Steffan-Dewenter & Tschamtké 2003)
	* Source/sink effects	Field study and ANOVA analysis
		(Haynes <i>et al.</i> 2007a; Haynes <i>et al.</i> 2007b; Kreyer <i>et al.</i> 2004)
Human population	* Connectivity indexes	Ring correlation
		(Carrière <i>et al.</i> 2004; Ricci <i>et al.</i> 2009)
		Multiple regression analysis
	Generalised linear models	(Diekotter <i>et al.</i> 2008; Ricci <i>et al.</i> 2009)
		(Pautasso & Powell 2009)

2.1 Overview of sampling methods

Sampling methods include direct observation, capture-mark-recapture (Kreyer *et al.* 2004), radiotelemetry (Vinatier *et al.* 2010), or interception trapping using pitfall traps (Botes *et al.* 2006), trunk traps (Rodeghiero & Battisti 2000), suction traps (Bommarco, Wetterlind & Sigvald 2007), and pheromone traps (Moral García 2006). Other methods are based on pest damage in agroecosystems (Augustin *et al.* 2007). Trapping data and pest damage data are considered to be "marked point processes", where traps or plants are mapped objects for which the number of trapped individuals or the intensity of attacks are recorded. Direct observations are considered as "point pattern processes", where the position of each individual is recorded on a two-dimensional Euclidian space. Trapping methods capture only a part of the real population, are generally affected by environmental factors, and they are often sex-biased, for example with pheromone traps. It is important to recognize that these limitations in sampling could affect our understanding of spatial heterogeneity.

2.2 Types of spatial population patterns

Spatial patterns are usually divided into three types: random, aggregated, or regular (Begon *et al.* 1996). Random distributions can be modelled by negative binomial or Poisson distributions (Desouhant, Debouzie & Menu 1998). Distribution patterns may also be of a gradient type (Judas, Dornieden & Strothmann 2002). Spatial patterns could be the result of the superposition of different types of patterns. Wiegand, Martinez & Huth (2009) found that spatial pattern of tropical tree species is composed of a random component and a component with two critical scales of clustering. This pattern can be modelled by Thomas processes (Thomas 1949) consisting of a set of clusters and points for each given cluster. Position of points relative to each cluster follows a bivariate Gaussian distribution, and position of cluster

can be randomly and independently distributed (single cluster). Clusters can be themselves clustered, leading to a double cluster.

The spatial distribution of populations can change across years, as illustrated by He & Alfaro (1997). The authors explained that white pine weevils were restricted to some trees early in the infestation (giving an aggregated distribution); the weevils then dispersed randomly to the other trees (giving a random distribution); and finally the weevils attacked all trees at the peak (giving a regular distribution).

2.3 Methods to define the kind of spatial pattern

For point pattern processes (see § 2.1, Overview of sampling methods), indices are mainly based on counts of individuals per unit of a grid, called quadrat. The simplest indices are based on the variance (S^2) and the mean (μ) of population density per quadrat. Lloyd's (1967) *mean crowding* is defined as $\mu^* = \mu + (S^2/\mu) - 1$ and represents the mean number per individual of other individuals coexisting in the same quadrat. *Patchiness* corresponds to the relative magnitude of spatial, quadrat-to-quadrat variations of population density (Kuno 1991). Taylor's *empirical power equation* $S^2 = a \cdot \mu^b$ makes it possible to assess the level of aggregation by means of slope b that indicates a uniform ($b < 1$), random ($b = 1$), or aggregated ($b > 1$) distribution of population (Arnaldo & Torres 2005). Morisita's *index of dispersion* (Morisita 1971) is based on the probability that two randomly selected individuals will be in the same quadrat. In addition, Iwao's *patchiness regression* (Iwao 1968) between mean crowding μ^* and mean density μ indicates the contagiousness inherent to the species (intercept of the regression) and the manner in which individuals distribute themselves in their habitat with change in the mean density (slope of the regression).

In contrast to the indices presented above, a statistical method termed SADIE® (Spatial Analysis by Distance IndicEs) (Perry 1995) takes into account spatial coordinates of quadrats. Given a number of individuals in each of several quadrats, two indexes can be computed from

this method: one referring to distance to crowding and one to distance to regular. The first SADIE® index is based on the total distance that individuals would have to move in order to get them all in one quadrat. The second SADIE® index is based on the total movement necessary to get the same number of individuals in each quadrat (Fortin & Dale 2005). SADIE® has been successfully applied to insect counts determined by regular trapping (Ferguson *et al.* 2003). Contrary to Taylor, Morisita, and Iwao indices, SADIE® is able to analyse counts of a given species at different times and counts of multiple species (Thomas *et al.* 2001).

Concurrently to methods applied at the quadrat scale, nearest-neighbour methods are used to analyse patterns of small populations at the individual level (Dodds, Garman & Ross 2006). For example, the Clark & Evans (1954) index gives a measure of dispersion. It is calculated as the ratio between the mean observed nearest-neighbour distance and the mean expected nearest-neighbour distance in case of randomness. The Clark & Evans Index cannot be computed when a large part of the area of observation is not classified because of missing values (Dodds *et al.* 2006). To test the occurrence of different patterns at different spatial scales within the same population, it is necessary to associate a goodness-of-fit test and the Pielou test to the Clark & Evans index, as shown by Potts & Willmer (1998) in their study of the spatial distribution of bee nests. The nearest-neighbour techniques gather the K -function (Ripley 1976) and its modified forms: the L -function usually defined as

$$L(r) = \sqrt{\frac{K(r)}{\pi}} \quad \text{for } r \geq 0 \quad (\text{Besag 1977}), \text{ and the pair correlation function } g(r) = \frac{dK(r)}{2\pi dr} \quad \text{for } r \geq 0$$

(Dietrich & Helga 1996). They help determining the radius r at which a collection of mapped points exhibits clustering (negative values) or overdispersion (positive values). As $K(r)$ is expected to be proportional to r^2 in planar case with deviations of interest for small values of r , the L -function has the main statistical and graphical advantage to be directly proportional to

r in planar case (Illian *et al.* 2008). The pair correlation function g has the advantage to isolate specific distance classes in a ring dr (Wiegand & Moloney 2004).

In contrast to point pattern processes, marked points processes include the abundance of population at each sampling point. It is relevant to employ spatial autocorrelation indexes that compares the similarity between pairs of sampling points within a given radius to randomly distributed pairs of points (Legendre & Fortin 1989). The spatial autocorrelation is described with Geary or Moran indexes (Legendre & Legendre 1998) and is represented in correlograms that show the relationship between autocorrelation and distance classes between sampling points (Legendre & Fortin 1989). Such indexes allow identifying patchy or gradient distributions and estimating the size of population patches. A particular case of marked point patterns includes the discrete number of individuals per host plant. The fit of frequency distributions on the total number of individuals per host plant (including the non infested ones) can be used to characterize spatial patterns (Warren, McGeoch & Chown 2003).

3. Identification of factors affecting spatial pattern

As emphasized by McIntire & Fajardo (2009), various processes can create the same spatial pattern, and therefore characterizing the spatial pattern is insufficient to elucidate the mechanisms that generated it. The possible role of exogenous or endogenous factors must be identified by statistical analyses (**Figure II-2: arrow 2 and Table II-1**). Biological factors such as species dispersal abilities, aggregation behaviour, or sexual attraction, and temporal variation of species population due to mortality and fecundity, could affect population pattern and will be illustrated in the part 4. Insects are affected by various environmental factors such as landscape composition, fragmentation of resource, or climate (Huffaker & Gutierrez 1999). Environmental factors are either continuous (e.g., temperature) or discrete (e.g., soil type).

3.1 Interpolation as a method to evaluate continuous environmental factors at unsampled locations

Kriging can be used to predict a continuous variable distributed in space or in time at unsampled locations based on data from sampled locations (Stein 1999). Temperature, an important driver of insect populations, is a good example of a variable that could require kriging because the density of climate stations is sometimes less than the resolution of the study (Aukema *et al.* 2008). The use of interpolated temperatures instead of temperature from the nearest climatic station helped Jarvis & Collier (2002) to model the phenology of pests in horticultural crops.

Stationarity is the major condition for applying kriging, i.e., mean and variance of the data must be the same throughout the area under study (Legendre & Fortin 1989). Ordinary kriging considers that values fluctuate locally and that stationarity is limited to local areas (Deutsch & Journel 1998). Interpolation can be performed for specific coordinates (punctual kriging) or for an area (blocked kriging) (Fortin & Dale 2005). More details on the kriging technique can be found in Cressie (1993).

Spatial variation of environmental variables can be interpolated using ‘trend surface analysis’ (Legendre & Legendre 1998) in which each variable is treated as a polynomial function of the longitude and latitude of the observation area. This method allows extracting simple spatial structures, such as gradient, a single wave, or a saddle. The sample area must be approximately homogeneous, and the sampling design must be close to regular (Norcliffe 1969). Moran's I eigenvectors are suited for extracting features at finer spatial scales than trend surface analysis (Dray, Legendre & Peres-Neto 2006; Griffith & Peres-Neto 2006).

3.2 Assessment of landscape elements

Landscape is considered as a mosaic of discrete spatial elements such as forest patches, field crops, or hedgerows. Landscape elements are usually represented as points, lines, or polygons

using a Geographic Information System (GIS) framework (Beckler, French & Chandler 2004). GIS helps to define their geometrical properties, like shape, edge length, and orientation, often established from aerial photographs. Such properties are important for assessing the effects of barriers or corridors on insect dispersal (Bhar & Fahrig 1998; Den Belder *et al.* 2002). Landscape composition can be evaluated by conducting in-person field surveys (Den Belder *et al.* 2002; Suzuki, Kawaguchi & Toquenaga 2007), by using satellite reflectance values to characterize vegetation types (Despland, Rosenberg & Simpson 2004), or color-infrared air photographs (Powers *et al.* 1999).

Investigating the connectivity between landscape elements and populations is simple when those elements are represented by lines (Holland & Fahrig 2000). Studying this linkage can be more complicated in the case of “polygons” or “patches” that refer to an area that encompasses elements of the same habitat type. A common practice is to calculate the connectivity between two patches as the product of the migration rate of the studied insect, the distance between the two patches and the area of the patches. The distance between two patches has been formalized by the spatial graph theory (Fall *et al.* 2007) that describes patch connectivity with nodes, links (connection between two nodes), and weights of link (accumulated "cost" along the link's line that reflects the cost of a movement along the line in terms of energy or of mortality risk). For example, patches are assimilated to their centres when patch area is small compared to the observation area of the study (Rabasa, Gutierrez & Escudero 2005); when patch area is large compared to the observation area, the distance between two patches is the nearest edge-to-edge distance (Diekotter, Billeter & Crist 2008). It is also possible to determine the area of each landscape element inside rings defined around each sampling location (Carrière *et al.* 2004; Ricci *et al.* 2009), providing a good description of source-sink effects of landscape elements. For example, Carrière *et al.* (2004) characterized Bt crops (i.e., crops that produce insecticidal proteins from the bacterium *Bacillus*

thuringiensis) as sinks of pink bollworms because of the drastic decrease of populations inside these elements, and characterized non-Bt crops as sources of pink bollworms.

3.3 Methods to link candidate factors to population patterns

Landscape features are assessed, and then they get the status of explanatory variables and are selected using various regression analyses. Spatial pattern, such as habitat fragmentation level (Haynes, Diekötter & Crist 2007a), can be assessed in a factorial design with replications. Effect of spatial pattern on population level is therefore evaluated through an analysis of variance (ANOVA) that helps studying interactions between variable. Explanatory variables could be selected by a stepwise procedure, as exemplified by Elliott *et al.* (1999) on factors affecting aphid predator populations, or with a Bayesian approach (Augustin *et al.* 2007). Generalized linear models (GLM) (McCullagh & Nelder 1989) are suited to non-normally distributed response variables. They put up with counts, proportions or occurrence data based on an appropriate choice of both statistical distribution representing the data (Poisson, Binomial, or Gamma distributions) and the link function relating the mean value of the response to a linear predictor (linear combination of explanatory variables). Beyond the GLM, the Generalized Linear Mixed Model is suitable for multiple scale analysis, as exemplified by Rabasa *et al.* (2005) on egg-laying of a butterfly assessed at the scales of patch, plant, and fruit.

The spatial-filtering method transforms a variable containing spatial dependence into one free of spatial dependence (Griffith & Peres-Neto 2006). The original data is partitioned into a spatial-filter variable capturing latent spatial dependency and a non spatial variable (Borcard, Legendre & Drapeau 1992). This flexible approach generates a very large number of spatial variables for which the most relevant ones need to be selected (Blanchet, Legendre & Borcard 2008). Among spatial-filtering methods described by Griffith and Peres-Neto (2006), the Principal Coordinates of Neighbour Matrices (PCNM) (Borcard & Legendre 2002) is based

on an eigenfunction decomposition of a truncated matrix of geographic distances among the sampling site. The resulting eigenvectors are considered as new variables that can be used in any statistical approaches (e.g. GLM, ordinary least square regression, canonical analyses such as redundancy or correspondence analyses). For example, Hamasaki *et al.* (2009) found spatial autocorrelation as the most important factor explaining odonate assemblages using PCNM, within-habitat environment and land use having comparable effects.

More specialized methods have been proposed to partition the spatial variation in species composition, defined as the "beta diversity" (Whittaker 1972), among environmental and spatial factors. Recently, Legendre, Borcard & Peres-Neto (2005) have compared two major methods in the domain, the Mantel approach (Legendre & Legendre 1998) based on distance matrices and canonical analysis operating on raw data, either canonical redundancy analysis or canonical correspondence analysis. They showed that the canonical approach is more appropriate to partition the spatial variation of species composition than the Mantel approach that underestimates the amount of explained variation. The Mantel approach, however, is appropriate to analyse variation in species composition among groups of sites.

4. Mechanistic modelling approaches

Mechanistic models deal explicitly with the processes underlying spatial patterns (**Table II-2**). According to Grimm *et al.* (2005), modellers have to find the optimal level of resolution, called the "Medawar zone", between a too-complex and a too-simple model. Discretizing the population, e.g., by considering age classes, the time, and the space increase the resolution of the model and, accordingly, its complexity. Subsequently, we focus on the capacity of models to account for the spatial arrangement of resources and the interaction among individuals, two key points of the spatial distribution of populations.

Table II-2. Overview of mechanistic models used to investigate spatial patterns of insect populations and corresponding references.

Topic	Method	References
Population spatial pattern results from...		
Insect behaviour		
* Dispersal	Lattice model	(Lee <i>et al.</i> 2007)
* Mate-finding behaviour	Individual-based model	(Byers 1991; Tyson <i>et al.</i> 2008)
* Aggregation	Metapopulation model	(De Gee, Lof & Hemerik 2008; Lof <i>et al.</i> 2008)
	Network model	(Yakob, Kiss & Bonsall 2008)
	Individual-based model	(Depickere <i>et al.</i> 2004)
	Cellular automaton	(Perfecto & Vandermeer 2008)
* Egg-laying tactic	Probabilistic model	(Gilbert <i>et al.</i> 2001; Horng 1997; West & Paul Cunningham 2002; Zu Dohna 2006)
	Individual-based model	(Byers 1996)
Habitat heterogeneity results from...		
Insect damages	Cellular automaton	(Bone <i>et al.</i> 2006; Kondoh 2003; Lee <i>et al.</i> 2007)
	Differential equations	(Lopes <i>et al.</i> 2010; Lopes <i>et al.</i> 2007)
	Individual-based model	(De Knegt <i>et al.</i> 2008)
Insect behaviour	Individual-based model	(Theraulaz & Bonabeau 1995)
Habitat heterogeneity affects population dynamics or population resistance to insecticide		
Landscape factors	Network model	(Yakob <i>et al.</i> 2008)
	Reaction-diffusion model	(Roques <i>et al.</i> 2008; Tyson, Thistlewood & Judd 2007)
	Individual-based model	(Arrignon <i>et al.</i> 2007; Parry <i>et al.</i> 2006)
	Leslie matrix model	(Benjamin, Cédric & Pablo 2008)
Climate factors	Lattice model	(Kizaki & Katori 1999)
	Individual-based model	(Arrignon <i>et al.</i> 2007; Parry <i>et al.</i> 2006)
Habitat fragmentation	Leslie matrix model	(Pichancourt <i>et al.</i> 2006)
	Cellular automaton	(Cerdeira & Wright 2004)
	Metapopulation model	(Fred <i>et al.</i> 2006; Hanski & Heino 2003; Kondoh 2003; Ovaskainen <i>et al.</i> 2002)

Planting management	Individual-based model	(King & With 2002; McIntire <i>et al.</i> 2007)
	Metapopulation model	(Banks & Ekbom 1999)
Resource quality	Individual-based model	(Levine & Wetzler 1996; Potting <i>et al.</i> 2005; Vinatier <i>et al.</i> 2009)
	Differential equations	(Helms & Hunter 2005)

4.1 Choice of modelling approaches in relation to the resolution of the model

Spatial patterns may be age-structured, and this calls for explicit consideration of age in corresponding models (Pichancourt, Burel & Auger 2006; Yoo 2006). In the contrary, models without consideration of age-structure are based on differential equations considering the population of insects as a whole (Lopes *et al.* 2007). The Leslie matrix (Williamson 1959) divides the population into different age classes and is based on transition probabilities from one class to another, based on mortality and fecundity ratios. Space can be included in these models, leading to a Multisite Leslie Matrix (Lebreton 1996) in which transitions from one habitat element to another are modelled (Pichancourt *et al.* 2006).

Space, another key point of model resolution, can be considered implicitly, i.e., the exact position of each habitat element or patch density can be considered to be unknown. Among them, metapopulation models such as the Levin's model (Levins 1969) calculate the number of sites occupied by a species. Dispersal is considered as unconstrained in implicit models, and local dispersal is therefore not considered (Tilman & Kareiva 1997). Implicit approaches are thus suitable for insect species with large dispersal capacities, such as winged species, or when local dispersal can be neglected. Lopes *et al.* (2010) developed an aphid model on this basis and reproduced observed population structure comprising both patches of highly infested plants for aphids that do not disperse and a spatially uniform distribution for long dispersers.

In spatially explicit models, the position of each habitat element, patch density, or individual is known. Among them, cellular automata are composed of a grid of cells with different states and are discrete in time, space, and state (von Neumann 1949). Cell states change according to transition rules and to their neighbourhood (Balzter, Braun & Kohler 1998). The lattice model (Hassell, Comins & May 1991) offers a more complex framework in which states of cells are directly linked to population densities simulated by differential

equations (Lee *et al.* 2007). As the lattice model, the network model (Yakob & Bonsall 2009) considers spatially located subpopulations with their own dynamics, but with variability in the connection structure of subpopulations. A very different category of spatially explicit models is that of reaction-diffusion models, which consider time, population, and space as continuous variables. They are suited for studying spatial patterns of invasion in systems with little or no spatial heterogeneity of resources (Roques, Auger-Rozenberg & Roques 2008).

When local movements and individual behaviour are considered as important processes affecting the spatial pattern, an individual-based modelling (IBM) approach will better describe the system, based on emergence of population properties from individual behaviour (Grimm & Railsback 2005). In IBMs, each individual is explicitly modelled and acts according to a set of rules depending on the landscape structure which is represented by a grid. Space and time are generally discrete. Because they have a high level of resolution, IBMs are parameter consuming, and the best combination of parameters that describes the spatial pattern must be selected to avoid exceeding the computation capacity.

4.2 Models as exploratory tools for studying the spatial arrangement of resources

The effects of habitat fragmentation on population dynamics can be studied by means of metapopulation models, considering group of sites that are suitable or unsuitable. They are well-suited for populations with large dispersal ranges relative to the landscape area (Ovaskainen *et al.* 2002). Metapopulation models, however, cannot be used to investigate the effects of element boundaries on movement or the effects of temporal variation in element quality (Pichancourt *et al.* 2006). More sophisticated models allow studying the effect of various spatial arrangements of plants on population dynamics, and therefore can be seen as 'virtual laboratories' (Charnell 2008). They can guide the arrangement of attractive, repulsive,

or resistant plants that are grown with a cultivated crop (Potting, Perry & Powell 2005; Tyutyunov *et al.* 2008).

4.3 Modelling interactions at the local or individual scale

Cellular automata and IBM are commonly used to represent interactions between individuals or between local populations of insects. Cellular automata are particularly suitable for modelling interactions between neighbours when dispersal is weak relative to the landscape area under study. The combination of a cellular automaton and a GIS environment is common (see Bone, Dragicevic & Roberts 2006 for an example on forest insect infestation). Using a cellular automaton, Kondoh (2003) showed that the spatial heterogeneity of a plant can lead to overgrazing by herbivores.

IBMs have been used to study aggregation by ants (Depickere, Fresneau & Deneubourg 2004) and fruit flies (Lof *et al.* 2008) as well as mate-finding behaviour of other insects (Byers 1991; Tyson *et al.* 2008). The elucidation of how individual behaviour affects the mating rate is relevant for the use of sterile insect techniques in the control of pest populations (Marsula & Wissel 1994). Yamanaka *et al.* (2003) used an IBM to investigate the effect of wind on pheromone trap efficiency and found that the modelled population clustered around the pheromone plume.

5. Linking spatial patterns and ecological processes

Spatial patterns of insect populations can be studied by inductive or deductive procedures (McIntire & Fajardo 2009). The inductive procedure characterizes the pattern and then suggests hypotheses about the underlying processes. The deductive procedure tests multiple hypotheses of underlying processes by comparing them with the pattern, either by experimentation or with mechanistic or statistical models. The aim of fitting a model to

empirical data is to gain an understanding of the pattern (Illian *et al.* 2008). Inferring processes from spatial patterns is a new approach motivated by advances in statistical and mechanistic modelling (Grimm *et al.* 2005; McIntire & Fajardo 2009) (**Figure II-2: arrows 3**). These two procedures are discussed in the following paragraphs. Few studies attempt to link statistical and mechanistic methods, regarding the references figuring both in **Table II-1** and **Table II-2** (Fred, O'Hara & Brommer 2006; Gilbert, Voulard & Grégoire 2001; Hanski & Heino 2003; Zu Dohna 2006).

5.1 Inductive procedure

Explaining a spatial pattern is sometimes reduced to the suggestion of processes from the characterization of the spatial pattern. For example, woodlots could physically restrict the dispersal of onion thrips and increase thrips mortality because of enhanced enemy abundance (Den Belder *et al.* 2002). The egg-laying decisions of *Apion onopordi* may reflect their limited dispersal abilities (Moravie, Borer & Bacher 2006). Broad *et al.* (2008) assumed that the spatial pattern of lepidopteran herbivores could result from interference with host location and egg-laying processes. In some cases, these suggestions merely require time to be further tested. However, testing complex mechanisms by means of models or experiments such as learning behaviour of insects (West & Paul Cunningham 2002) or the Allee effect (Takasu 2009) appears a hard task.

5.2 Deductive procedure using empirical studies

In some cases, the type of spatial pattern detected suggests underlying simple mechanisms that motivate empirical studies. For example, Chamorro-R *et al.* (2007) used nearest-neighbour analyses to determine that the spatial distribution of males of *Panacanthus pallicornis* tended toward randomness or uniformity; based on this pattern, the authors hypothesised that the spacing of males was due to the calling song. They validated this

hypothesis by studying dispersal of two groups of released males, one group with torn tympanic membranes and the second with intact tympanic membranes. Ellis (2008b) estimated that the spatial distribution of offspring of the tree mosquito was aggregated. Using both a capture-mark-recapture study and the same spatial indices, he then compared different scenarios for explaining the roles of habitat selection, passive aggregation, and egg-laying preference in the spatial population patterns.

5.3 Deductive procedure using statistical models

McIntire & Fajardo (2009) proposed a new approach, called "Space as a surrogate", that combines mechanism and statistical models for inferring processes from spatial patterns. The approach is based on (i) the determination of all the relevant processes affecting the system under study, (ii) the development of the resulting spatial patterns these processes would create, and (iii) the comparison of these hypothesised, process-based patterns with the real patterns. For example, McIntire (2004) tested multiple hypotheses concerning the spatial pattern of the mountain pine beetle and found that factors such as weather and surface vegetation affected the boundary formation of beetle outbreaks. This framework helps the researcher to infer mechanisms without additional empirical study. Finally, the framework should be applied to the construction of multiple hypotheses around processes, e.g., random or correlated walks, long or weak dispersers, aggregative or repulsive behaviours.

Autoregressive models combine *per se* mechanism and statistical methods. They are well suited for modelling the abundance of species whose distributions are controlled by a combination of exogenous factors and biological properties (Lichstein *et al.* 2002). The spatial autoregressive process can occur (i) only in the response variable ("lagged-response model"), (ii) both in response and predictor variables ("lagged-mixed model"), (iii) only in the error term of the model ("spatial error model") (Dormann *et al.* 2007). Such models can account for ecological processes, such as density dependence (Bjørnstad, Liebhold & Johnson

2008; Bommarco *et al.* 2007), spatial dependence of the population at neighbouring locations (Kadoya *et al.* 2009), or both spatial and temporal dependencies (Aukema *et al.* 2008). The regression also includes exogenous factors concerning climate (Aukema *et al.* 2008) or landscape composition (Kadoya *et al.* 2009). These autoregressive models usually provide a better prediction of the population distribution than simple regression (Latimer *et al.* 2006). Autoregressive models may be unsuitable for very large georeferenced data sets because of computation time required for analysing distance matrices (Griffith & Peres-Neto 2006).

5.4 Deductive procedure using mechanistic models

Because a spatial pattern is the result of ecological processes, it is interesting to compare patterns emerging from simulations of those processes with real data. Following "Pattern-oriented modelling" approach (Grimm *et al.* 2005), "single working hypothesis" models are constructed and their confrontation to data can lead to the acceptance or rejection of the hypothesis (Arrignon *et al.* 2007; Fred *et al.* 2006; Hanski & Heino 2003; Parry, Evans & Morgan 2006; Vinatier *et al.* 2009). When there is a good fit of modelled to real results, it may be difficult to know whether the processes and parameters of the model are relevant because a different set of processes and parameters could simulate the same pattern. When there is a poor fit of modelled to real results, the rejection of the hypothesis does not confirm any particular alternative hypothesis, as emphasized by McIntire & Fajardo (2009).

A further understanding of spatial patterns can be obtained by determining whether alternative models reproduce the observed pattern (Grimm *et al.* 2005), models failing to reproduce the observed spatial pattern being rejected. The objective of this approach is similar to that of the "space as a surrogate" framework described above for statistical models. Gilbert *et al.* (2001) illustrated this approach in the study of distribution of attacks of *Dendroctonus micans* by both Morisita's index of dispersion and a probabilistic model. Among a choice of

scenarios, the best fit was obtained for the hypothesis of induced host susceptibility following random attack.

Pattern-oriented modelling can also reduce the uncertainty of parameter estimates by estimating parameters that reproduce different patterns simultaneously. This technique, which is known as "inverse modelling", was used by Vandermeer *et al.* (2008) to study the spatial distribution of ant clusters. The authors constructed a cellular automaton based on two parameters, ant clusters expansion and mortality, and they used both population density over time and cluster size distribution as criteria for the estimation procedure.

6. Conclusion

Spatial patterns of insect populations depend on various factors reflecting the behaviour of individuals and the spatial organisation of habitat patches. Among methods used to understand spatial patterns, statistical models are widely used to link population levels with habitat traits in a descriptive way, leading to a better knowledge of habitat preferences of insect species. Mechanistic models offer the possibility to understand the mechanisms resulting in population patterns, and to evaluate the role of habitat and other factors. Inferring those processes from patterns relies on a judicious combination of methods, especially of statistical and mechanistic models that can be combined in an iterative process. Statistical models are used to identify factors influencing the spatial distribution. When factors are identified, statistical or mechanistic models are used to understand which mechanism is related to those factors and how it influences the spatial pattern. Simulated patterns are compared to observed patterns using similar statistical indexes.

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CHAPITRE III – MESURE DE LA DISPERSION DES ADULTES DE *C. SORDIDUS*.

L'hétérogénéité spatiale des populations peut être liée à des facteurs biotiques, comme la capacité de dispersion des individus et leurs relations avec l'hétérogénéité spatiale de leur environnement. Sélectionner les facteurs biotiques affectant la dynamique spatiale des populations nécessite de trouver des méthodes adéquates de suivi des individus. Les avancées récentes des méthodes de télémétrie et notamment la miniaturisation des puces électroniques permettent d'aborder ces questions sous un angle nouveau.

Ce chapitre repose sur l'article publié dans *Animal Behaviour* et intitulé **Radiotelemetry unravels movements of a walking insect species in heterogeneous environments**. L'objectif est de présenter une méthode originale de suivi d'un insecte marcheur et d'identifier les facteurs affectant la distribution spatiale des adultes de charançon. Il était nécessaire de choisir un marqueur adapté au déplacement du charançon. Le choix d'un marqueur dépend des caractéristiques morphologiques et comportementales de l'espèce étudiée et également de la question de recherche posée. Dans le cas du charançon et de l'analyse du mouvement, il s'agissait de trouver une méthode de suivi permettant de multiples recaptures sans perturber l'individu, ce qui éliminait le marquage visuel par peinture ou scarification. La méthode devait permettre un suivi individuel, ce qui éliminait le suivi par radar harmonique (Riley et al. 2007), et être applicable à un insecte de petite taille, ce qui éliminait les puces RFID (Radio Frequency Identification) actives (Hedin and Ranius 2002). En l'état actuel de nos connaissances dans le domaine, seules les puces RFID passives satisfaisaient à l'ensemble des critères.

Afin d'identifier les facteurs responsables de la distribution spatiale des charançons, nous avons caractérisé les trajectoires individuelles en utilisant des statistiques circulaires (**Figure III-1**). Les facteurs endogènes et exogènes sont sélectionnés *a priori*, puis sont testés au regard des principales statistiques de mouvement des trajectoires. Dans le cadre de notre étude, il s'avère que le facteur exogène "Organisation paysagère" a une grande influence sur les statistiques de mouvement, à l'inverse des autres facteurs endogènes et exogènes. L'**Annexe A** figurant en fin de thèse représente les cartographies des trajectoires de l'ensemble des essais conduits lors de la thèse (seuls les essais B1, B2 et B4) ont servi dans cette partie.

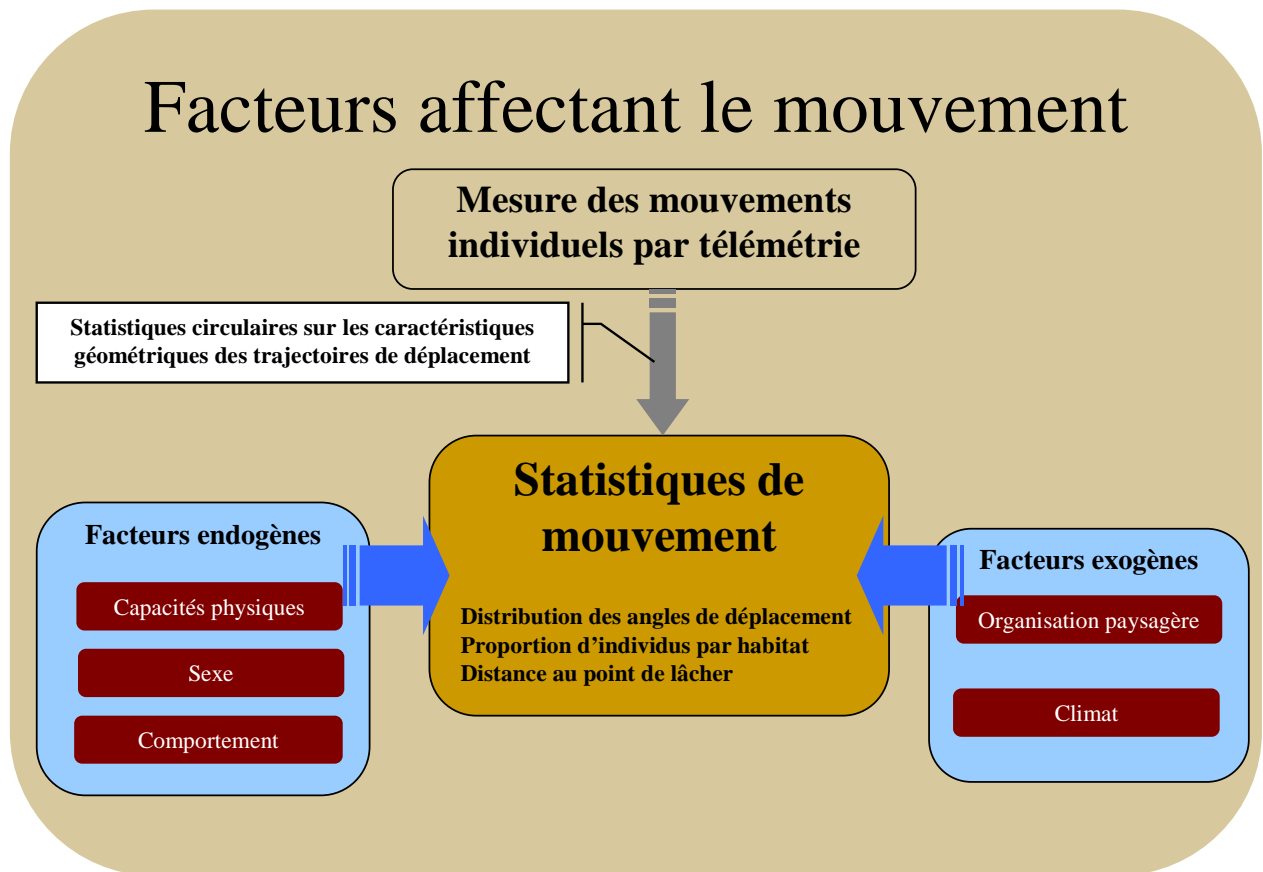


Figure III-1. Schéma présentant la démarche d'identification des facteurs agissant sur le mouvement.

Radio telemetry unravels movements of a walking insect species in heterogeneous environments

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Abstract

The study of movements of individual organisms in heterogeneous environments is of primary importance for understanding the effect of habitat composition on population patterns. In the present study, we developed a new experimental methodology to measure individual movements of walking insects, based on radio tracking. Our aims were to understand the link between habitat heterogeneity and moving patterns, and to characterize the movements with dynamic models of diffusion. We tracked individual movements of adults of *Cosmopolites sordidus* (Coleoptera: Curculionidae) with passive radio frequency identification (RFID) tags under different field management practices. Diffusion models on recapture data indicated a subdiffusive movement of this species. Great variation was found between individual paths, but this variation was not sex-dependent. Movement of released *C. sordidus* was affected by banana planting pattern and the presence/absence of crop residues but not by the presence of a cover crop between rows of bananas or by banana variety. These results show that the RFID technology is useful for evaluating the dispersal parameters of cryptic insects in heterogeneous environments.

Keywords:

RFID, tracking, dispersal, habitat preference, *Cosmopolites sordidus*, circular statistics.

1. Introduction

The dispersal of individuals is a fundamental process affecting the metapopulation dynamics of organisms (Chapman et al. 2007). Dispersal affects foraging choices, habitat selection and home ranges (Clobert et al. 2004). Dispersal allows population spread and redistribution between patches of suitable habitat (Doak 2000; Stacey & Taper 1992). Dispersal varies according to size, geometry and suitability of patches (Kreyer et al. 2004; Tschamntke et al. 2002). Dispersal explains part of spatial patterns of populations, such as clumping (Lopes et al. 2007; Vandermeer et al. 2008). Good measurements of individual dispersal behaviour in the wild are therefore needed to address these ecological processes (Samietz & Berger 1997). Movement processes inform on foraging ecology of organisms (Ramos-Fernandez et al. 2004). Fitting movement processes on quantitative data allows predicting long-distance dispersal and therefore assessing population persistence and cohort strength (Coombs & Rodriguez 2007).

Most studies of insect dispersal are based on mark-recapture techniques, where insects are trapped and checked for the presence of the marker (Arellano et al. 2008; Cronin et al. 2000; St Pierre et al. 2005). Simple methods such as paint (St Pierre & Hendrix 2003), ink, dust, or mutilations (Delattre 1980) are used for visual marking of insects (Hagler & Jackson 2001). Regular tracking of the same individuals is impossible due to the fact that insects need to be trapped for identification. Other methods allowing regular tracking exist, such as direct observation by eye (Banks & Yasenak 2003) or with video recording (Hardie & Powell 2002; Robinson et al. 2009; Sendova-Franks et al. 2010) for diurnal organisms as well as artificial illumination, fluorescent powders (Turchin & Thoeny 1993) or reflective material for nocturnal organisms (Kindvall 1999). Tracking methods should account for individual variability in movement, which is influenced by sex, age, or gene pool. For example, dispersal can be sex-biased (Gros et al. 2009) or highly variable between individuals of the same sex (Bengtsson et al. 2004).

Among the methods for studying individual movement patterns of organisms, the radio frequency identification (RFID) tagging is the most promising technology. It is a wireless sensor technology, based on the detection of electromagnetic signals emitted by a tag. It can be used to detect tags through a variety of habitats, e.g., a layer of soil (Mociño-Deloya et al. 2009). This method allows tracking organisms regularly in time and with limited disturbance of their behaviour, keeping the individual information of movements. RFID tags may be active (i.e., with a built-in battery) or passive (i.e., based on the electromagnetic field generated by the RFID reader) (Domdouzis et al. 2007). Detection distance ranges from several centimetres for passive tags to several hundreds of meters for active tags. It is only during the last decade that radio transmitters have become sufficiently small to be attached to invertebrates (Reynolds & Riley 2002). Active tags have been used on tarantulas (Janowski-Bell & Horner 1999) and large insects (Hedin & Ranius 2002; Lorch et al. 2005; Riecken & Rath 1996). Passive tags have been used on social insects such as bumblebees (Molet et al. 2008) or honeybees (Streit et al. 2003), and also on walking insects such as ants (Robinson et al. 2009) to study activity patterns.

Until now, RFID tags have not been used to study dispersal parameters of walking insects in their natural environment, such as the banana weevil *Cosmopolites sordidus* (Germar). This insect attacks only wild and cultivated clones of the genus *Musa* (banana, plantain, abaca) and is recognized as a major pest of banana crops (Gold et al. 2001). The adult has a long life span and low fecundity; it is nocturnally active and gregarious. Banana weevils are hygrotactic (Roth & Willis 1963) and prefer habitats with a high humidity such as banana plants and crop residues (Gold, 2001). Males emit an aggregation pheromone that attracts both males and females (Beauhaire et al. 1995). Although *C. sordidus* adults have functional wings, they never have been observed flying and are assumed to move only by crawling (Gold et al. 2001). The movement of *C. sordidus*, however, has not been studied in detail. The insect's

cryptic, nocturnal behaviour does not allow the use of direct visual marking techniques. Furthermore, *C. sordidus* has limited dispersal abilities (Gold et al. 2001). Banana fields can be infested with *C. sordidus* through the planting of infested material, through spread from a heavily infested neighbouring field, or through adults that have survived the last planting, which result in random, linear, or patchy distributions, respectively (Delattre 1980; Treverrow et al. 1992). *C. sordidus* is able to colonise new banana plants from heavily infested plants.

We present here a new experimental methodology, based on radio-tracking and quantitative analyses of individual movement paths. We applied this method to a cryptic insect to address the following questions: (i) Which movement process best suits the movement patterns of a walking insect? (ii) How does habitat heterogeneity influence the spatial orientation of this organism? The study was conducted on *C. sordidus*, which shows cryptic and walking behaviours, in a heterogeneous natural environment composed of banana plants, bare soil, crop residues (leaves, pieces of old pseudostems, and shoots), and cover crops.

2. Material and methods

2.1. Insect trapping, sexing, and marking

Because *C. sordidus* was difficult to rear in the laboratory, adults were obtained from the field. Accordingly, instead of using cohorts of known age, we used large sets of individuals directly collected with pseudostem traps from one banana field (Rivière-Lézarde, Martinique, West Indies). Pseudostem traps consisted in cutting banana plants in slices and laying them on the ground to attract weevils. This sampling method has been largely used in biological studies on *C. sordidus* (Delattre 1980; Kiggundu et al. 2007). We assumed that the distribution of ages of sampled individuals was similar to that of the field population. Insects were sexed according to Longoria (1968), based on punctuations of the rostrum that differ for

male and female. Before they were released in experiments, insects were kept in the laboratory for ≤ 1 week in large plastic boxes (80 x 40 x 40 cm) with soil and pieces of pseudostem at room temperature. In order to prevent crowding effects we kept 25 adults per piece of pseudostem, which was much less than the density of weevils found on infested plants (Delattre 1980; Gold & Bagabe 1997). They were marked 2 h before release with passive RFID tags (ref: TXP148511B, Biomark Inc) that were attached to the insect by braided fishing line (Daiwa 14 kg, 0.260 mm). Cyanoacrilate glue (super glue[®]) was used to adhere the tag to the line and the line to the insect's back (**Figure III-2**), and epoxy glue (Araldite[®]) was used to smooth the surface of the tag. We attached the tag to the insect's back to avoid disturbing insect burrowing behaviour. The ratio of tag mass/individual insect mass was 1:1 and the width of the tag was narrower than the insect. Each tag and therefore each insect was individually labelled with a unique identification label.



Fig. III-2. An individual *C. sordidus* with its tag.

2.2 Laboratory experiment

Insects with and without tags were followed for short distances (0.5 m) in controlled conditions at 25°C to evaluate the possible bias due to tag weight on dispersal capacities of insects. Forty adults (20 tagged + 20 non-tagged) were released in the morning (1000 hours

local time, Martinique: GMT - 5 h) at the centre of a 1-m² wooden board that was covered or not covered with crop residues. The experiment was conducted separately for males and females and for boards with and without crop residues. For each individual, the time from release to arrival at the end of the wooden board was measured. Then recorded individuals were immediately removed. The release was repeated three times both for the covered and non-covered treatments, yielding a total of 120 individuals tested.

2.3 Field experiments

2.3.1 Characteristics of experimental plots

Three experiments (named exp.1, exp.2, and exp.3) were conducted in banana fields in Martinique, French West Indies (**Table III-1**). Banana plants are considered to be semi-perennial, and plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner 1994). Lateral shoots are selected by farmers so that there is only one shoot per mat. Mats of banana plants consist of one plant in young plantations and several plants in older plantations; mats include shoots, the so-called mother plant, and the base of old plants resulting from former cycles. Banana plants were planted in double row in exp.1 (**Figure III-3a, b**) (width of row: 1 m, width of inter-row: 5 m) and in staggered rows (width of inter-row: 2 m) in exp.2 and exp.3 (**Figure III-3c-g**).

Table III-1 Characteristics of field experiments.

	Experiment 1	Experiment 2	Experiment 3
Site name	Rivière-lézarde	Petit Morne	Petit Morne
Site location	14°39'N, 60°58'W	14°37'N, 60°58'W	14°37'N, 60°58'W
Field area (m ²)	2400	1300	1300
Area per plot (m ²)	400	100	100
Plantation	Double row	Staggered rows	Staggered rows
Number of banana planting cycles	4	1	1
Banana stage	Flowering	Flowering	Flowering
Design	Randomized complete block	Randomized complete block	Randomized complete block
Treatments	2	4	4
Number of replicated plots/treatment	3	3	3

Experiment 1 was carried out between January and February 2009 on a 4-year-old banana field. The objective of exp.1 was to evaluate the effect of cover crop on insect dispersal. Experiment 1 included two treatments: with and without cover crop in the inter-row; each treatment was represented by three replicate plots.

Experiments 2 and 3 were carried out on banana fields recently planted with three varieties: *A* (*Musa spp.*, AAB group, cv. Créole Blanche); *B* (*Musa spp.*, AAA group, cv. FLHORBAN 924); and *C* (*Musa spp.*, AAA group, cv. Cavendish Grande Naine). *A* is susceptible and *C* is tolerant to immature stages of *C. sordidus*; *B* is intermediate (Kiggundu et al. 2003).

The objective of exp.2, which was carried out between May and June 2009, was to test the effects of banana plant variety on dispersal capacities and habitat preference of *C. sordidus*. The varieties *A*, *B*, and *C* were planted in pure stands (one plot per variety) and in a plot containing a random mixture of the three varieties; all plots in exp.2 had bare soil (**Figure III-3**). These four kinds of plots were replicated three times, giving a total of 12 plots.

The objective of exp.3 was to test the effect of different spatial arrangements of crop residues (homogeneously distributed or in stripes) on weevil movements. We compared the absolute angles of weevils released on bare soil (outside residues) for plots planted with varieties *A*, *B* or *C* in pure stands with residues in stripes (**Figure III-3f, g**; 5 and 4 replications, respectively) to the absolute angles of weevils released in the same relative places in plots planted with a random mixture of varieties, where residues were homogeneously distributed (**Figure III-3e**; 3 replications). Distribution of absolute angles was expected to be non-directional when crop residues were homogeneously distributed over the plot, and oriented toward crop residues when residues were in stripes. Experiment 3 was carried out between July and August 2009.

We tested the effect of climate variables on movement patterns. Temperature, rainfall, wind strength and relative humidity of air were $26.2^{\circ}\text{C} \pm 1.6$ (mean \pm SD), $6.7 \text{ mm d}^{-1} \pm 10.5$, $1.62 \text{ m s}^{-1} \pm 0.34$, and $75.3\% \pm 5.2$, respectively. We found no significant effect of climate variables on the percentage of recaptured tags, the mean distance moved per day and the number of movements during the experiments (Pearson-test > 0.05). The only exception was an effect of the relative humidity of the air on the distance moved per day ($R^2 = 0.20$, $N = 40$).

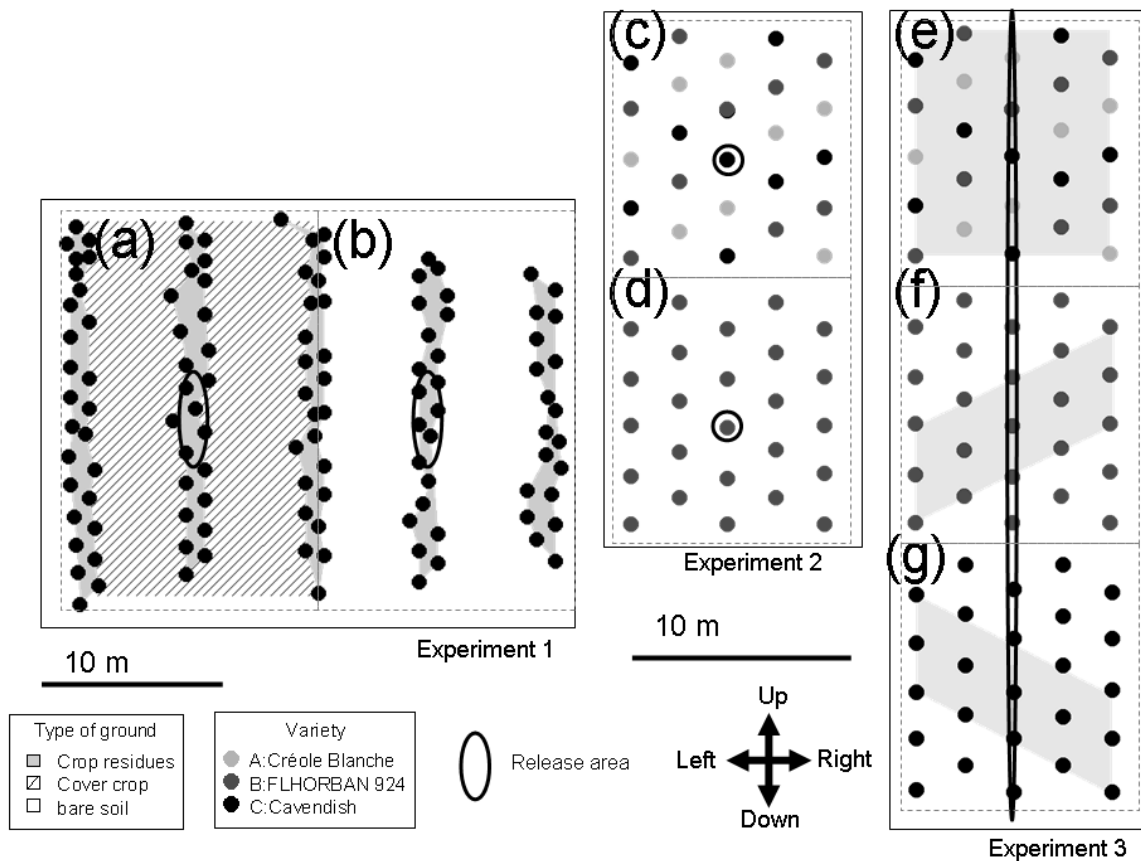


Figure III-3. Diagrams of the three field experiments used to measure the effects of various factors on movement of *C. sordidus* individuals with RFID tags. An example of each treatment is presented (a-g). Treatments a-e, f, and g are replicated three, five, and four times, respectively. Dashed lines indicate plot edges. Experiment 1 compared the effects of a cover crop (a) or bare soil (b) between the banana rows. Experiment 2 compared the effects of banana varieties planted in a random mixture (c) or in pure stands (d, where variety B is shown as an example). Experiment 3 compared the effects of crop residues covering the whole treatment area (e, with mixed varieties) or arranged as a strip (f and g, with varieties planted in pure stands). Black ellipses represent the release area of each experiment; *C. sordidus* individuals were released in a patch, a plant, and on a line in exp.1, exp.2, and exp.3, respectively.

2.3.2 Releasing and monitoring of the tagged insects

For exp.1, 204 tagged individuals (34 per plot) were released on 12 January 2009. Insects were released in the center of each plot on a patch 2 m long and 0.3 m wide in the double row (**Figure III-3a, b**). For exp.2, 360 tagged individuals (30 per plot) were released on 11 May 2009. Insects were released near the central banana plant of each plot, on a circle of one meter diameter (**Figure III-3c, d**). For exp.3, 360 tagged individuals (30 per plot) were released on 16 July 2009. Insects were in a line with alternate male and female individuals spaced by 20 cm (**Figure III-3e, f**). Orientation of the weevils' body on the ground and sex of released weevils were random for the three experiments.

Insect location was monitored during 38, 22, and 30 days for exp.1, exp.2, and exp.3, respectively. Individuals were monitored daily during the first week, three times per week during the second week, two or three times per week the following weeks, and one time the last week of the experiment leading to 18, 13, and 16 measures for exp.1, exp.2, and exp.3, respectively. A RFID antenna with a Destron Pit tag reader (model FS2001 FR/ISOCB) was used to locate insects at the base of banana plants, on the surface of bare soil, and on the surface of soil covered with crop residues. The detection distance, which was measured in the field with tags alone, was between 0 and 20 cm. When a tag was detected, the power of the signal increased with the proximity to the tag; the precision of the signal's position was 10 cm. A stake with its code was sunk at immediate proximity of the tag position, and this position was indicated on a 1/100 map of the observation area, with an overall precision of 30 cm. Each tag was spatially localized, and its environment was recorded. For exp.1, the recorded environments were 'near a banana', 'on a mother plant', 'on a shoot', or 'on an old plant'. For exp.2, the recorded environments were 'on bare soil' or 'on a mother plant'. For exp.3, the recorded environments were 'on bare soil', 'under the crop residues', or 'on a mother plant'.

At the end of each experiment, all the tags were systematically searched for and removed from the field. The state of each tag was recorded (attached to a living weevil, attached to a dead weevil, or separated from the weevil).

2.3.3 Analysis of insects paths

Basic geometric and quantitative properties of the path of each insect were defined according to Patterson et al. (2008) as follows. A path consists of several segments, named steps, linking time-indexed positions of an individual over the study period. Paths were located on an orthogonal plane with plot axes (left-right and up-down) as indicated in **Figure III-3**. We calculated the length of each step, the length of the path, the absolute angle between the segment linking begin and end of the path and plot axes, and the relative angle (called the turning angle) between two successive steps, as well as the mean squared displacement between each step (R_n^2). Lengths of steps were divided by time (in days) between two successive observations to take into account unequal times between observations. For individuals found alive at the end of the experiment, the monitoring period stopped at the end of the experiment. For individuals found dead or not found at the end of the experiment, the monitoring period stopped at the last recorded movement. Movement metrics and all parameters were calculated taking into account individual monitoring periods, the monitoring period of each individual being defined as the time between release and the last recorded movement. Movements of length less than ten centimetres were not recorded.

For testing the movement process that best suits the movement patterns of *C. sordidus*, we plotted the mean squared displacement (R_n^2) of each individual versus time (t) and we tested whether the diffusion model was rather subdiffusive or superdiffusive by fitting a power model on the curve of the resulting curve:

$$R_n^2(t) = at^b \quad \text{Eq. 1}$$

where a and b are parameters. The coefficient b of the power model indicates whether the curve is concave or convex, suggesting a subdiffusive or a superdiffusive movement, respectively (Uchaikin 1999; Yadav & Horsthemke 2006).

Model of **Eq. 1** was fitted to the data using Nonlinear Least Squares (Bates & Watts 1988). The coefficient R^2 of the fitting was estimated using a log-transformation of the data for linearization (Turchin & Thoeny 1993).

2.4 Statistical analysis

All statistical analyses were performed with R software (R Development Core Team 2009) using basic packages, and specialized packages such as "spatstat" (for spatial analyses and mapping) and "circular" (for circular analyses).

The effect of the tagging method (tagged or non-tagged) on the dispersal capacity (laboratory experiment) was assessed using a t-test, after testing the normality of the data with the Shapiro-test (Royston 1982). Repeatability of recapture rates over time was calculated from a one-way analysis of variance using among-plots and within-plots variances (Lessells & Boag 1987).

Distributions of movement metrics for male and female over the three field experiments were compared using the Kolmogorov-Smirnov test (Conover 1971). The Watson-two test was used to compare the circular distribution of angles (Jammalamadaka & SenGupta 2001). Mean and standard deviation of absolute and relative angles were calculated assuming von Mises distributions. This assumption was confirmed by the Watson test (Stephens 1970). The significance of mean direction of circular distributions was tested using the Rayleigh test (Jammalamadaka & SenGupta 2001). For applying circular statistics, bimodal distributions of absolute angles in exp.1 and exp.3 were separated in two ranges, from -180° to 0° and from 0° to 180° .

Reaching a given row with or without a cover-crop and being attracted towards a given variety were considered as Bernoulli experiments for statistical analyses. The effect of adding a cover crop on the proportion of individuals that reached the next row on the other side of the release point was analysed with a generalized linear model (GLM), assuming a binomial distribution of values. The global effect of varieties on movement metrics of insects was analysed with a GLM, assuming a Poisson distribution of number of movements during the experiment (Kolmogorov-Smirnov test, $D = 0.1231$, $P = 0.71$) and a Gamma distribution of distance moved per day (Kolmogorov-Smirnov test, $D = 0.0739$, $P = 0.41$). The deviation from a theoretical distribution of the observed distribution of weevils on varieties in plots planted with a mixture of varieties was χ^2 -tested to analyse the attractiveness of varieties to weevils.

3. Results

3.1 Efficiency of the tagging method

Results of laboratory experiment (tagged vs. non-tagged insects) are presented in **Table III-2**.

For both non covered or for the covered wooden boards, there was no significant difference for time to reach the edge of the wooden board between tagged and non tagged both for females, and males. We also observed that tagged weevils maintained in boxes with pseudostem pieces were able to enter and leave the pseudostem freely.

The percentage of recaptured tags was $77.2 \pm 6.4\%$ (mean \pm SE), $56.4 \pm 13.2\%$, and $61.3 \pm 6.7\%$ for exp.1, exp.2, and exp.3, respectively (**Figure III-4**). Repeatability of percentage of recaptured tags over time was 0.35, 0.57, and 0.14 for exp.1, exp.2, and exp.3, respectively. The lowest level of repeatability for exp.3 was due to a weak decrease of the recapture rate the first days (data not shown).

Table III-2 Time for individual weevils to reach the edge of the wooden board in the laboratory experiment.

	Tagged individuals				Non tagged individuals			
	Mean	Range (min-max)	Mean	Range (min-max)	df	t-test	P	95% Confidence interval
Non covered experiment								
Female	13.1 min	(2.4 – 25.0 min)	13.2 min	(3.2 – 23.4 min)	118	0.1133	0.91	(-1.6 – 1.8 min)
Male	12.0 min	(2.5 – 23.0 min)	11.0 min	(1.6 – 24.3 min)	118	-1.043	0.30	(-11.0 – 12.0 min)
Covered experiment								
Female	357.7 min	(40 – 574 min)	344.5 min	(58 – 585 min)	118	-0.496	0.62	(-65.7 – 39 min)
Male	357.7 min	(40 – 574 min)	326.7 min	(40 – 595 min)	118	-0.346	0.73	(-44.5 – 63.4 min)

Mean times were normally distributed (Shapiro test, $W = 0.9833$ and 0.9691 , $P = 0.006$ and $P < 0.0001$ for non covered and covered experiments, respectively).

3.2 Dispersal parameters of *C. sordidus*

The individual monitoring period was 21.3 ± 11.5 days. A large proportion of individuals remained in the 2-m area around the release site after 3 days (0.74). This proportion decreased to 0.43 after 29 days. Individuals moved on average 0.37 m.d^{-1} for the three experiments, considering the ratio between path length and monitoring periods over all individuals. When periods of inactivity were removed, this rate of movement increased to 0.50 m.d^{-1} . The maximal distance covered was 9 m in one day. The distribution of distances moved per day was not significantly different between males and females for the three experiments (Kolmogorov-Smirnov test, $D=0.0455$, $P=0.78$).

The power model of **Eq. 1** explained 85% of the variation of the mean squared displacement (Nonlinear Least Squares, R^2 on log-transformed data). As $0 < b < 1$ (95% confidence interval estimated from 1,000 bootstraps : (0.44-0.67)), the curve was concave (**Figure III-4**) and the movement subdiffusive.

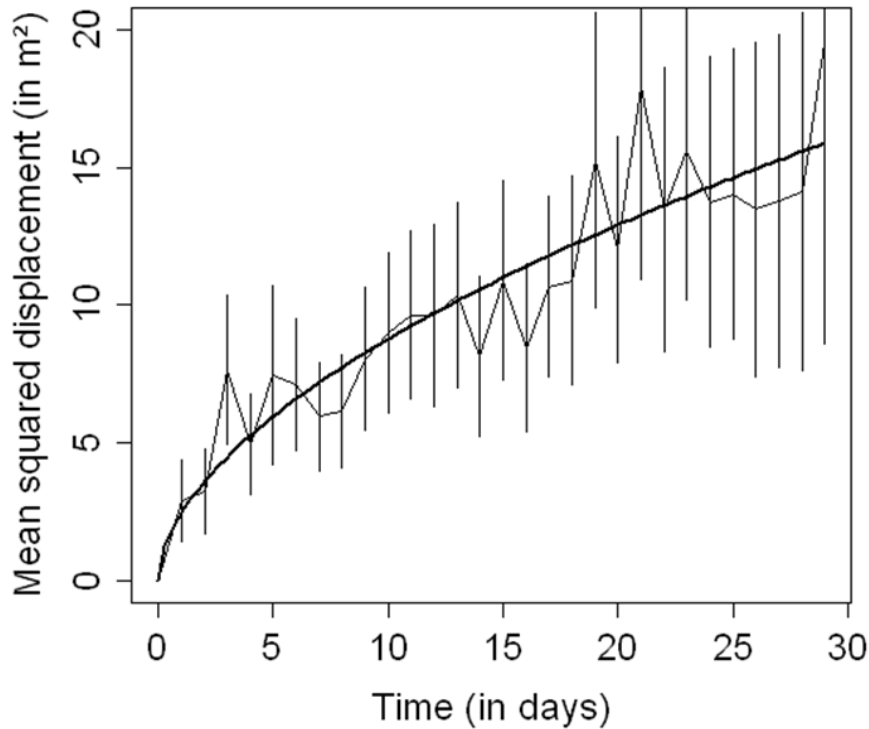


Figure III-4. Fit of a power model (Eq. 1) on mean squared displacement of individuals versus time since release. Error bars (SE) are indicated.

Regarding the proportion of individuals in each habitat (bare soil, banana plant, and crop residues), in exp.1, the proportion of individuals in crop residues decreased over time (Pearson's product-moment correlation, $r_p = -0.65$, $df = 16$, $P = 0.003$). The proportion of individuals in mother plants and in old plants was equal ($\chi^2_1 = 0.14$, $P = 0.71$) and considerably larger than the proportion in shoots ($\chi^2_1 = 420$, $P < 0.0001$) (**Figure III-5a**). In exp.2, all the individuals were found in planted bananas. In exp.3 nearly 60% of the individuals were found in crop residues, about 40% were found in planted bananas consisting only of mother plants, and none were found on bare soil (**Figure III-5b, c**). Furthermore, the proportion of males in crop residues increased over time at the expense of the proportion in planted bananas (Pearson's product-moment correlation, $r_p = 0.87$, $df = 13$, $P < 0.0001$).

(Figure III-5c). The proportions of females in crop residues and on banana plants did not change over time in exp.3 (Pearson's product-moment correlation, $df = 14$, $P = 0.88$) (Figure III-5b).

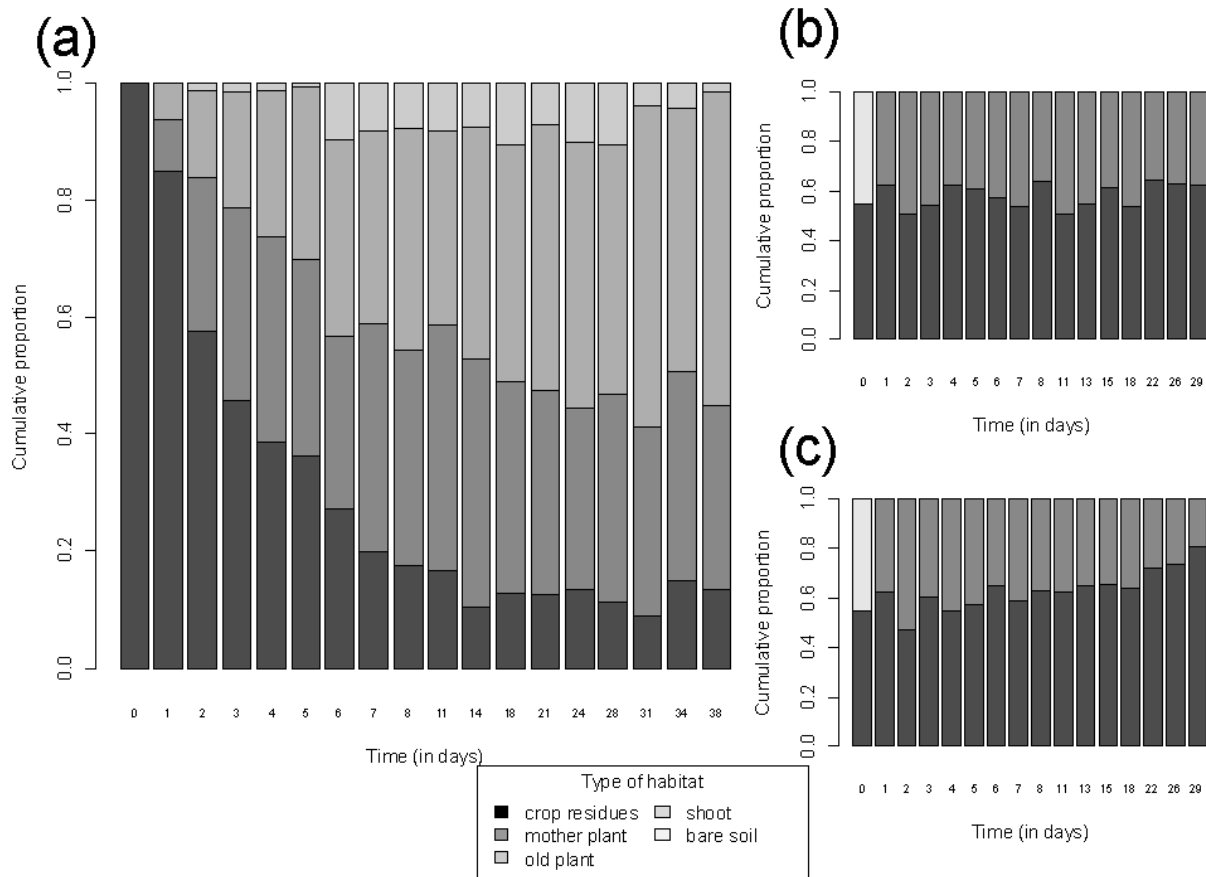


Figure III-5. Relative cumulated histograms of distributions of released individuals of *C. sordidus* in different habitats in exp.1 (a) and exp.3 (b, females and c, males).

The distribution of turning angles between successive positions differed significantly from a uniform distribution for every experiment (Watson-two test, test statistic = 0.217, 0.648, and 2.203 for exp.1, exp.2 and exp.3, respectively; $P < 0.001$). Turning angles were back-oriented in the three experiments at $179.1^\circ \pm 45.2^\circ$ (mean direction of resultant vector \pm circular variance, Rayleigh test, $P < 0.001$), indicating a tendency of weevils to do U-turns (Schtickzelle & Baguette 2003). Their distribution was not significantly different between males and females (Watson-two test, test statistic = 0.0001, $P > 0.10$).

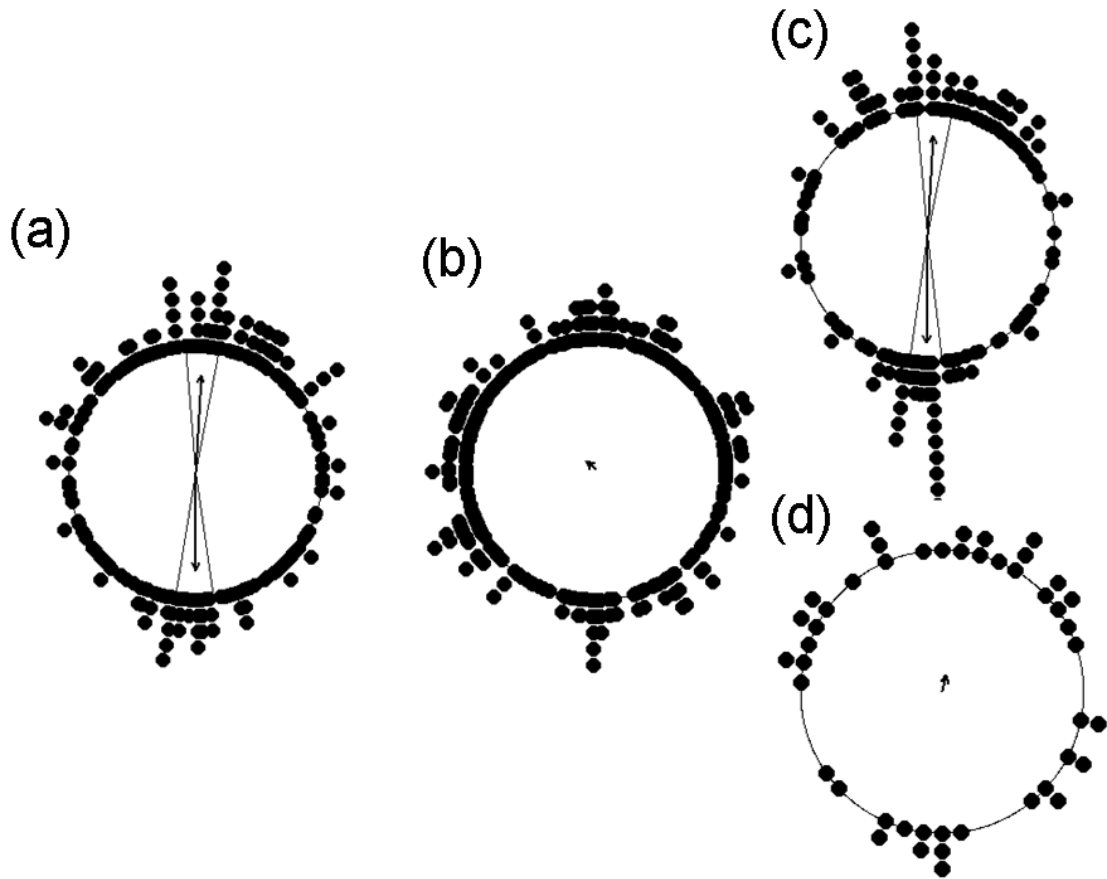


Figure III-6. Frequency distribution of absolute angles between individual paths of *C. sordidus* and plot axes for exp.1 (Figure III-3a-b) (a, n=198), exp.2 (Figure III-3c-d) (b, n=284), and exp.3 for individuals released on bare soil (Figure III-3f-g) (c, n=155) or in the same relative places under crop residues (Figure III-3f-g) (d, n=46). Arrows represent the mean direction of circular distributions. For (a) and (c), distributions are separated in two ranges (see material and methods). Confidence intervals (0.95) are figured by black lines, excepted for (b) and (d) where the distribution of angles does not differ from a uniform distribution.

3.3 Effect of management practices on movement patterns of *C. sordidus*

In exp.2 and exp.3, in which varieties A, B, and C were planted homogeneously, the variety had no effect on the movement metrics of the insect, such as the number of movements during the experiment (GLM, $F_{2,62} = 0.79$, $P = 0.59$) and the mean distance moved per day (GLM, $F_{2,281} = 0.62$, $P = 0.43$). In the treatment where a random mixture of those varieties was planted, the proportion of individuals moving from the release point to a different variety was cumulated over repetitions, yielding $P_A = 11/31$, $P_B = 8/31$, and $P_C = 12/31$. These proportions

were not significantly different from the proportions of the variety in the plot (1/3) ($\chi^2_3 = 1.82$, $P = 0.61$).

At the end of exp.1 weevils were significantly more abundant in their release row than in other rows ($\chi^2_1 = 19.3$, $P < 0.001$). There was no effect of the type of inter-row (bare soil or cover-crop **Figure III-3a, b**) ($\chi^2_5 = 1.67$, $P = 0.89$) on the weevils that moved to another row. The absolute angles between paths of each individual and plot axes differed according to the experiment (**Figure III-6**). In exp.1, paths of released individuals were oriented up and down (**Figure III-6a**, mean direction = -85.2° and 82.3° for negative and positive angles, respectively, Rayleigh test, $P < 0.0001$), following the organization of planting rows. In exp.2, the distribution of absolute angles between individual paths was not significantly different from a uniform distribution (**Figure III-6b**, Watson-two test, test statistic = 0.105, $P > 0.1$). In exp.3, the distribution of absolute angles for individuals released on bare soil was significantly different from a uniform distribution (**Figure III-6c**, Watson-two test, test statistic = 0.179, $P < 0.01$). Mean direction of individuals released on bare soil was -90.5° and 86.3° for negative and positive angles, respectively (**Figure III-6c**, Rayleigh test, $P < 0.0001$). In contrast, the distribution of absolute angles for individuals released under crop residues was not different from a uniform distribution (**Figure III-6d**, Watson-two test, test statistic = 0.0422, $P > 0.1$).

4. Discussion

The new RFID based methodology was successfully used to understand true fine-scale movements of an insect species in heterogeneous environment. First, the laboratory experiment showed that the tagging method did not affect movements of *C. sordidus*, although the weight ratio of tag/insect was almost 1/1. This ratio is generally lower for flying insects in marking-recapture studies, ranging from 0.05 to 0.025 (Ranius 2006). However, *C.*

sordidus is a burrowing insect and is able to carry more than its weight, as is also the case for ants, which carry from 3.5 to 6.5 times their body weight (Burd 2000). Furthermore, the estimated frequency and range of dispersal movements were of the same magnitude as those estimated in the other marking-recapture studies on this insect. In our experiments, 74% of the weevils remained near their release site after 3 days, in accordance with Delattre (1980). The dispersal of *C. sordidus* appeared to be limited and slow. Adults moved on average 0.37m.d^{-1} , with a maximal distance moved in one day of 9 m, which agrees with a maximal weevil movement of 6 m and 15 m recorded by Wallace (1938) and Cendana (1922), respectively. After 29 days, weevils had remained within 10 m of the release site. Whalley (1957) and Cardenas & Arango (1987) reported that most banana weevils move less than 10 m over a period of several months. Secondly, recapture rates were higher than found with capture-recapture studies (Koppenhofer et al. 1994; Tinzaara et al. 2005). The error in location of individuals (0.3 m) was negligible in comparison to the range of displacements (1 to 10 m). However, RFID-tagged weevils may suffer from long term effects such as exhaustion or a higher level of predation, which were out of the scope of this study that focused on short-term movements. For example, tagged weevils could be more visible to predators (toads, lizards or birds) when they disperse on bare soil or egg-laying behaviour of females could also be influenced by the tagging. Further experiments will be needed to study this potential bias.

The relationship between the mean squared displacement and time since release was not linear as predicted by a simple diffusion model (Banks & Yassenak 2003). The analysis of this relationship revealed that the movement process of *C. sordidus* is subdiffusive rather than diffusive. This means that weevils are the most active just after release. During this period, weevils may search for a suitable micro-habitat.

The analysis of the circular distribution of turning angles characterizes the foraging strategies of *C. sordidus*. It suggested that individuals make frequent U-turns. As plots were

surrounded by deep and large ditches and no weevils were found inside, U-turns could be attributed to weevils that hit the plot borders. Nevertheless, the high level of circular variance ($\sigma^2 = 45.2^\circ$) of turning angles means that subsequent steps of trajectory were poorly correlated, indicating a random walk movement of individuals. The high frequency of turns suggests an 'area-restricted' searching behaviour (Westerberg et al. 2008). This type of behaviour is usual when individuals are entering a resource patch (Dajoz 2002; Garnier et al. 2009; Shuranova 2008).

Radio tracking revealed variation among individuals for movements and habitat selection. As shown by the error bars of mean squared displacements over time, some individuals moved faster than others. Individuals did not choose necessarily the same habitat whereas they were released at the same position (data not shown). However, individual variation in movement and in habitat selection was not explained by gender. Movement parameters seemed generally similar for males and females, in accordance with Gold et al. (1999). Hedin et al. (2008) found the same result with *Osmoderma eremita*. The sex ratio is balanced for both *O. eremita* (Ranius 2001) and *C. sordidus* (Gold et al. 2001). Differences in movement patterns are generally observed for organisms with a biased sex ratio. Higher movement rates are found for males when the population is female-biased (Gruber & Henle 2008; Kwiatkowski et al. 2008; Young 2001). In our experiments, however, we found fewer tagged males than females in banana plants. It is thus possible that females were less exposed to predators than males, perhaps because females must lay eggs in the less-exposed parts of the banana corm to increase the survival of immatures. We supposed that a part of individual variability of insect path is determined by other factors than gender, such as age, or fitness.

Our study suggests that habitat matrix heterogeneity affects movement patterns of insects. Attractiveness of habitats increases with the stage of the resource, as shoots of banana plants that are less attractive than older plants. Attractiveness of some habitat varies temporally, as

crop residues for old banana plantations. The analysis of absolute angles between subsequent steps of individuals clearly indicates that the spatial heterogeneity of plantation and the spatial organisation of residues affect the direction of individual paths. As movements of individuals are oriented toward crops and residues, spatial arrangement of these elements may alter dispersal. However, some habitat elements, such as cover crop or varieties of banana in our case, do not affect weevil's dispersal, which is consistent with McIntyre et al. (2004), who showed no effect of adding mulch on infestation patterns of *C. sordidus* in Uganda and with Pavis and Lemaire (1997), who suggested that the resistance of varieties was not related to attractiveness but rather to antixenosis.

In conclusion, we developed an experimental methodology that makes it possible to study the fine-scale movements of walking insects at the individual level, to derive movement patterns and to analyse the effects of habitat heterogeneity on movements. This offers the opportunity to implement individual-based models for pattern-oriented modelling (Grimm et al. 2005) such as that of Vinatier et al. (2009) on *C. sordidus*, thus contributing to bridge the gap between individual and population studies.

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CHAPITRE IV – INTEGRATION DE L'HABITAT-DEPENDANCE DANS LA DISPERSION DES ADULTES DE *C. SORDIDUS*

Le mouvement est un processus encore difficile à quantifier et à caractériser à l'aide d'outils statistiques classiques. Il doit être décomposé en un ensemble de mécanismes élémentaires plus facilement analysables. L'étude expérimentale de la dynamique spatiale du charançon (Chapitre III) a révélé des capacités de mouvement limitées avec une orientation des déplacements très dépendante des éléments du milieu. Cette partie a pour but de préciser les liens entre mouvement et habitat afin d'intégrer ce processus dans un modèle individu-centré. Il sera ainsi possible de tester des configurations d'habitats variables affectant le mouvement du charançon du bananier.

Ce chapitre repose sur l'article soumis à *The American Naturalist* et intitulé **Should I stay or should I go? Habitat-dependent dispersal kernel improves prediction of movement**. Son objectif est de présenter une nouvelle manière de décomposer le mouvement individuel en se basant sur la calibration des paramètres du mouvement par maximum de vraisemblance. Plusieurs hypothèses de décomposition du mouvement sont testées en utilisant soit un modèle mécaniste (carré orange), soit un modèle statistique de comparaison de vraisemblance (carré bleu) (**Figure IV-1**). Les estimateurs des potentiels des habitats du modèle mécaniste sont évalués en minimisant la vraisemblance du modèle statistique (flèche pointillée). La meilleure hypothèse de décomposition du mouvement est sélectionnée (flèche grise) sur la base des deux approches (statistique et mécaniste). Dans notre cas d'étude, il semble que le mouvement se décompose le mieux en un processus markovien qui tient compte du potentiel de préférence de l'habitat de destination **et** d'une perception de l'espace dépendante de l'habitat de départ. Les essais ayant été utilisés dans cet article sont désignés par B1, B2, B4, J1 et J2 dans l'**Annexe A** de fin de thèse.

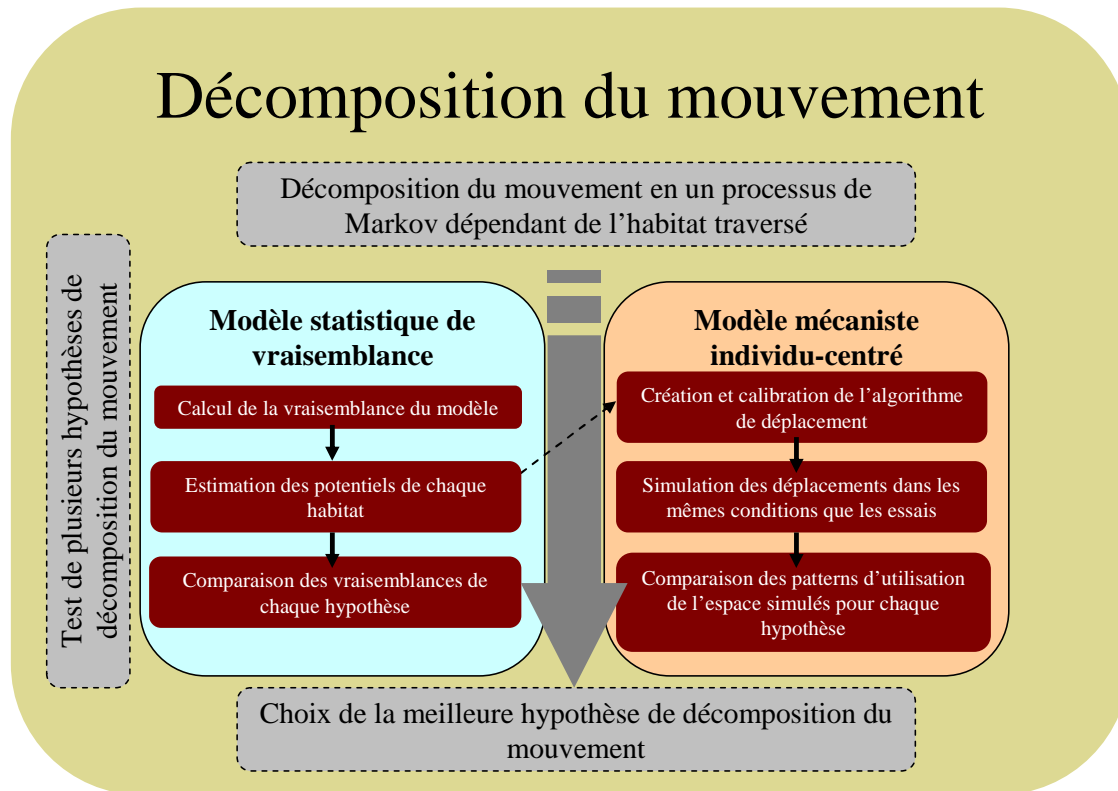


Figure IV-1. Schéma de la démarche de décomposition du mouvement.

Should I stay or should I go? A habitat-dependent dispersal kernel improves prediction of movement

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Abstract

Ecologists require a better understanding of how animals move in heterogeneous environments. An animal's decision to leave a location or to stay is driven by spatial context and its perceptual range. The perceptual range of individuals, which is formalized by dispersal kernels that account for costs and constraints to select a location anywhere, is generally considered as invariable. However, an animal's perception could be spatially affected. We constructed a model of movement as a first order Markov chain in which movement depends on the habitat characteristics of current and target locations. We applied the approach to a radio-tracking data set of a walking insect's. We tested hypotheses of independence of the individual's current location on its perceptual range using likelihood comparisons and Pattern-Oriented modeling. The results demonstrate that dispersal kernels should take into account the current habitat and the value of combining statistics and modeling for clarification of spatial processes.

Key words: Space use, dispersal kernel, spatial explicit model, pattern-oriented modeling.

1. Introduction

In heterogeneous environments, animal movement and habitat selection are determinants of the dynamics and spatial distribution of populations (Lima and Zollner 1996). Features of target habitats and perceptual ranges of animals, i.e., how habitat is assessed relative to the animal's location, influence the animal's decision to move (Matthiopoulos 2003). Animals use a wide variety of chemical, visual, and acoustic cues to assess the suitability of habitat for providing food (Searle et al. 2005), egg-laying (Rabasa et al. 2005), or protection from predators (Huffaker and Gutierrez 1999).

Discrete choice models redefine an individual's habitat preference after each movement or relocation of an individual (Fortin et al. 2005; Rhodes et al. 2005) based on its perceptual ranges. The perceptual range of an individual represents an “information window” onto the greater landscape, where either all habitat locations are equally available (Arthur et al. 1996) or their availabilities are defined via “dispersal kernels” that account for the costs and constraints of moving to another location depending on its distance to the current location (Lindström et al. 2008; Rhodes et al. 2005). Kernels can have flexible shapes depending on a set of parameters whose values may have important consequences for the spatial distribution of organisms (Chapman et al. 2007b). For example, a fat-tailed distribution allows more long-distance dispersal events and consequently represents a larger perceptual range than a thin-tailed one (Kot et al. 1996).

Dispersal kernels have commonly been considered as static through time and space (Chapman et al. 2007b; Coombs and Rodriguez 2007). Observational evidence indicates, however, that dispersal kernels may differ according to time (Phillips et al. 2008); intrinsic factors such as sex, age, social status, or energy reserves; and environmental conditions such as climate, season, habitat quality, competition, predation, and parasitism (Bianchi et al. 2009; Walters et al. 2006).

In this study, we hypothesized that perceptual range, defined by a negative-exponential kernel with one parameter β , might be influenced by habitat features of the animal's current location. We constructed a model of movement as a first order Markov chain in which arrival and departure locations of individuals depend on habitat characteristics and their distance from individual's current location. We tested a habitat-independent kernel, in which β is constant, and a habitat-dependent kernel, in which β depends on the habitat of the departure cell, in two ways. First, using a radio-tracking data set, we compared the likelihoods of the models of movement including the two alternative kernels. Second, we applied the Pattern-oriented modeling (POM) approach (Grimm et al. 2005) to compare the performances of the two kernels using a spatially explicit individual-based model. POM is a validation procedure that focuses on characteristics of space use. In this procedure, simulated values of each alternative model are compared to several observed patterns, and POM discriminates models that fail to reproduce the patterns (Grimm et al. 2005). POM is based on an emerging principle of individual-based models, and according to this principle, population-level pattern is the result of individual behaviours (Grimm and Railsback 2005). The POM procedure helps researchers evaluate the assumptions implicit in ecological models. We illustrated our approach using a data set of the locations of the coleopteran *Cosmopolites sordidus* in heterogeneous environments (Vinatier et al. 2010a). To obtain the data (i.e., to monitor the fine-scale movements of insects), we used recent advances in the radio-tracking of individuals (Schick et al. 2008).

2. Methods

2.1. Study species and radio-tracking data set

The beetle *Cosmopolites sordidus* moves by walking, and its activity is nocturnal and cryptic. It occurs in all countries where its only host plant, the banana, occurs (Gold et al. 2001). Adults prefer moist environments and feed on banana plants and banana plant residues. Females lay eggs at the base of the host plant, and the larvae grow inside the corm. Gender has no known effect on movement of *C. sordidus* (Vinatier et al. 2010a).

The radio-tracking data set was derived from five plots (Appendix A) in which the pattern of habitats was a mosaic that was experimentally manipulated. We distinguished four habitat types that were mutually exclusive: (*P*) host plant, (*C*) crop residues, (*B*) bare soil, and (*D*) ditch. *P* and *C* are considered suitable for *C. sordidus* while *B* and *D* are considered unsuitable. Each plot was defined as a grid of 1-m² cells with one habitat type ascribed to each cell. The cell size was chosen to characterize resource variability, following Marzluff *et al.* (2004), and to match radio-tracking precision (Vinatier et al. 2010a). Plots 1 and 2 contained a high proportion of unsuitable habitats while Plots 3-5 contained a high proportion of suitable habitats (Appendix A). The radio-tracking data set consisted of daily observations of cell-to-cell movement of approximately 600 males and 600 females of *C. sordidus* that were released in the five plots and followed for at least 1 week.

2.2. Overview of the approach

We chose discrete space-time formalism and used a dispersal kernel that depends on the individual's current location. The environment was represented by a grid of $k = 1, \dots, m$ discrete cells with their own habitat type. We rounded the position of individuals to one-meter grain, i.e., each individual movement was considered as a discrete walk inside the grid.

Individual movements were considered to be dependent on the habitat characteristics and/or distances but independent of time. The probability of moving from cell a to cell b per unit time was a first-order Markov chain defined as:

$$\Pr(a \rightarrow b) = \frac{\alpha_{h(b)} f_{\beta_h}(d_{ab})}{\sum_{k=1}^m \alpha_{h(k)} f_{\beta_h}(d_{ak})} \quad \text{Eq. 1}$$

where $\alpha_{h(k)}$ is the relative preference for habitat h of cell k , d_{ak} is the distance between cells a and k , and $f(d_{ak})$ is the dispersal kernel (which is dependent on distance d_{ak}). We chose $f_{\beta}(d_{ab}) = \exp(-\beta \cdot d_{ab})$. This negative exponential distribution is the most commonly used kernel because its shape depends on only one parameter. Two alternative kernels were tested: a habitat-independent (but distance-dependent) kernel where β_h is constant and a habitat-dependent kernel where $\beta_{h(a)}$ depends on the habitat h of the departure cell a .

2.3. Parameter estimation

Parameters of the two alternative models of movement were obtained by maximum likelihood estimation. The likelihood, L , of $i=1, \dots, n$ movements from cell a_i to cell b_i was defined as:

$$L = \prod_{i=1}^n \frac{\alpha_{h(b_i)} f_{\beta_h}(d_{a_i b_i})}{\sum_{k \neq i} \alpha_{h(k)} f_{\beta_h}(d_{a_i k})} \quad \text{Eq. 2}$$

The unknown parameters α_h and β_h were estimated by minimizing the negative log-likelihood of Eq. 2, $l = -\ln(L)$, using Nelder's Mead method (Nelder and Mead 1965). The estimation was constrained, i.e., the sum of alphas was equal to 1, and each parameter was positive. The estimation used the data of all plots taken together because we hypothesized that model parameters are independent of the spatial configuration of the plots.

The two models with df_1 and df_2 degrees of freedom, respectively, were compared by a likelihood-ratio test using a χ^2 with $(df_1 - df_2)$ degrees of freedom.

2.4. Pattern-oriented modeling

Once parameterised, the alternative hypotheses of movement were implemented following the POM procedure in a stochastic and spatially explicit individual-based model (Vinatier et al. 2009). In this condensed version, environment is a grid or collection of cells of various habitats; each individual moves from one cell to another at fixed time intervals and makes a discrete choice between the n cells of the grid. This choice was based on a multinomial probit model in which the probability p that a particular cell is chosen is determined by the dispersal kernel f_β and the target-habitat preference α .

For each plot, predictions of the two bottom-up models, generated by 100 runs for the same population, were compared to observed values of the radio-tracking data set for two variables describing use of space: (i) proportion of individuals staying at their release cell at the end of the study period, which depends on the suitability of their environment, and (ii) distribution of dispersal distances, which depends on the sinuosity of travel path and on the suitability of the traversed habitat. The first variable was compared (predicted vs. observed) with the Kolmogorov-Smirnov test (Stephens 1970), and the second variable was compared with the Chi-square test.

3. Results

When four distinct habitats were considered and likelihood estimation was used, the relative ranking and values of target-habitat preference estimates (alphas) were similar for the habitat-independent and habitat-dependent models. Host plant and crop residues were equally

preferred, whereas bare soil and ditch were much less preferred (**Table IV-1**). The likelihood of the habitat-dependent model was significantly greater than that of the habitat-independent model (Table 1, χ^2 , df= 7, $P<0.001$). When habitat types are pooled, the likelihood was either similar or reduced for both models; the likelihood was similar for the habitat-dependent model when habitats, host plant, and crop residues were pooled (χ^2 test, df= 5, $P=0.61$) and reduced for all other cases (χ^2 multiple test, df= 1 to 7, $P<0.001$). The habitat-dependent model was always better than the habitat-independent model (χ^2 multiple test, df= 1 to 7, $P<0.001$). Regarding parameter β (which defines the shape of the dispersal kernel), the higher the value of β_i for the current habitat i , the more the individual stayed in habitat i . The value of β_i was highest for the host plant or the crop residues, intermediate for the bare soil, and lowest for the ditch (**Table IV-1**). Consequently, the movement rate was highest when the current habitat was ditch, was intermediate for bare soil, and was the lowest for crop residues and host plant (**Figure IV-2**). The value of parameter β of the habitat-independent model was close to that of parameters β for host plant or crop residues in the habitat-dependent model (**Table IV-1**).

Table IV-1. Modified Likelihood [-2.log(L)] and parameter estimates for each model using the *C. sordidus* calibration data set. In a pair of rows, numbers in bold indicate the best model regarding modified Likelihood, and numbers in italics refer to the habitat-dependent model.

Dispersal kernel parameters				Preference parameters				-2.log(L)	
Habitat-independent model		Habitat-dependent model							
Four habitats									
	β_P	β_C	β_B	β_D	α_P	α_C	α_B	α_D	
1.62	0.54	0.43	0.018	0.008	0.54	0.40	0.036	0.014	12991
	2.01	2.11	1.14	0.71					12394
Three habitats with Host plant+Covered soil									
	β_{P+C}	β_B	β_D		α_{P+C}	α_B	α_D		
1.63	0.95	0.01	0.04		0.91	0.02	0.07		12991
	2.04	1.09	0.74						12395
Three habitats with Ditch+Bare soil									
	β_P	β_C	β_{B+D}		α_P	α_C	α_{B+D}		
1.62	0.55	0.43	0.02		0.56	0.41	0.03		12993
	1.97	2.14	1.08						12422
Two habitats: Host plant+Covered soil and Ditch+Bare soil									
	β_{P+C}	β_{B+D}			α_{P+C}	α_{B+D}			
1.63	0.97	0.03			0.94	0.06			13014
	2.04	1.08							12445
A single habitat: Host plant+Covered soil+Ditch+Bare soil									
	$\beta_{P+C+B+D}$				$\alpha_{P+C+B+D}$				
1.89					0.25				14769

Note: For subscripts of parameters: P, host plant; C, covered soil; D, ditch; B, bare soil. P+C means that host plant and covered soil habitats are pooled in a single category.

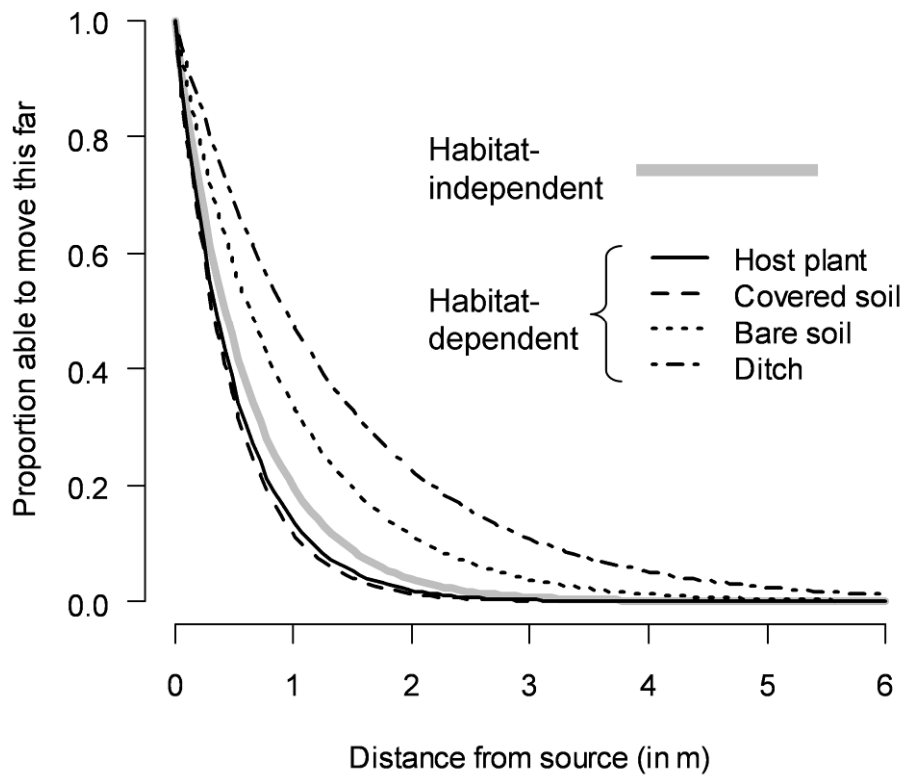


Figure IV-2. Fitted via likelihood maximization of negative exponential kernels $f(d)=\exp(-\beta.d)$ for the habitat-independent model (grey line) and the habitat-dependent model (black lines). For black lines, the shape of the curves depends on the value of β , i.e., on the type of habitat at the current location.

For the POM procedure, the habitat-independent model underestimated the proportion of individuals staying at their release cell in Plots 4 and 5 (**Figure IV-3**). It overestimated the dispersal distances in all plots except Plot 2, in which it underestimated the dispersal distance (**Figure IV-4**). In contrast, the habitat-dependent model accurately simulated all the characteristics of space use. The only exception was for the distribution of dispersal distances in Plots 1 and 5 according to the Kolmogorov-Smirnov test despite corresponding simulated and observed distributions were close to each other (**Figure IV-4**).

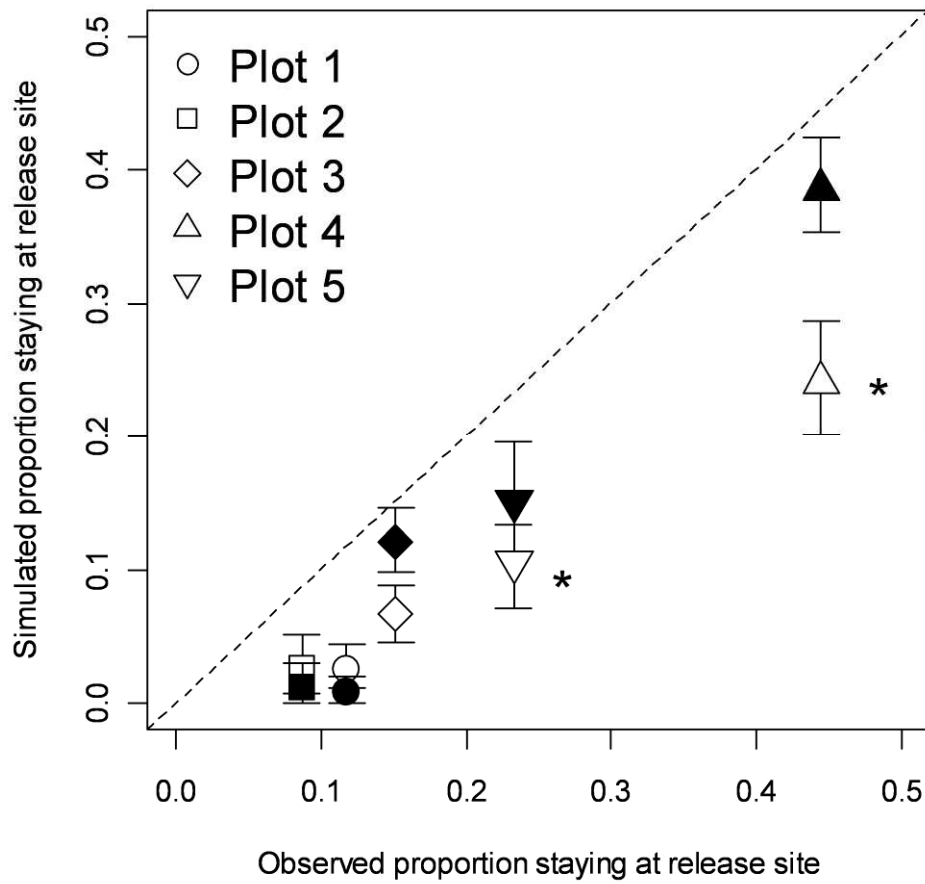


Figure IV-3. Proportion of individuals staying at their release site at the end of the study period as simulated using the POM procedure. Means (points) and 95% quantiles over 100 simulations (segments) are shown for values simulated with the habitat-independent model (white) and the habitat-dependent model (black). The dotted line corresponds to a perfect fit between observations and simulations. Stars indicate that simulations are significantly different from observations (χ^2 test, $df=1$, $P<0.01$).

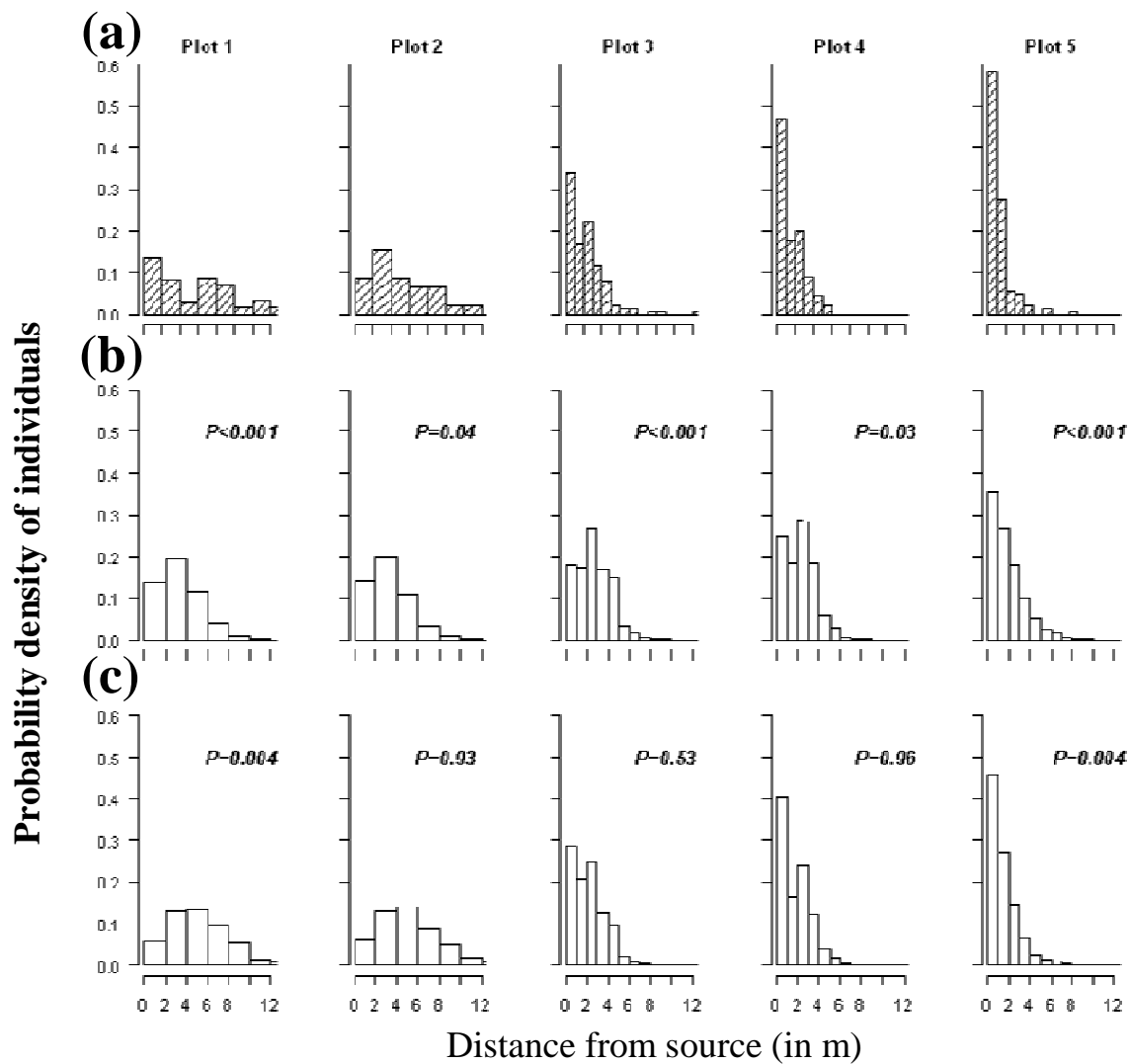


Figure IV-4. Observed and simulated ranges of dispersal distances over the study period for five plots. Simulations were based on two dispersal models and analysed by the POM procedure. (a) observed results, (b) simulated results from the habitat-independent model, and (c) simulated results from the habitat-dependent model. P-values correspond to the results of the Kolmogorov-Smirnov test that compared the distribution of observations vs. a set of 100 simulations.

4. Discussion

In this study, which used the walking insect, *C. sordidus*, we developed a stochastic Markov model of movement and demonstrated the value of taking into account the effects of both target and departure habitats. The ranking of estimated habitat preferences (α_i) was coherent with the *a priori* quality of habitats of *C. sordidus*: the host-plant is the most attractive for feeding and egg-laying, and the litter-covered soil for protection against predators and

feeding. Bare soil and ditch are less attractive because they are too dry and offer no physical protection against birds or other generalist predators. The ranking of estimates for parameter β_i , which describes the effect of departure habitat, was similar to that of the α_i , indicating that an attractive habitat is one where the probability to stay is high.

Following Rhodes *et al.* (2005), who highlighted that movement probabilities could be a function of habitat, our results suggest that incorporating habitat dependency in dispersal kernels of spatially explicit models greatly improves the prediction of movement. Furthermore, our pattern-oriented modeling approach showed that a habitat-independent model failed to predict important characteristics of animal space use. A habitat-dependent dispersal kernel is relevant because it enables reasonable prediction of the spatial behaviour of animals in both low and high suitability areas.

Lima & Zollner (1996) indicated that perceptual range is linked to the species and depends on mortality risk of dispersing animals. According to the authors, relative to animals with a high perceptual range, animals with a low perceptual range can expect a higher risk of mortality because they spend more time searching for a suitable habitat. In our study, individuals located in an unsuitable habitat (bare soil or ditch) experienced a high risk of predation and consequently would increase their perceptual range to reach a protective habitat such as host plant or litter-covered soil. On the other hand, individuals located in a suitable habitat had a low mortality risk and might decrease their perceptual range and spend more time in their current habitat. Our study highlights that individuals adapt their movement probability to their current location; this is in accordance with Huffaker & Gutierrez (1999), who argued that many insects modify their movement pattern to remain in favourable areas. The use of a mechanistic model helps in the study of complex processes, such as the plasticity of perceptual range.

The Markov chain of the dispersal model was constructed with the assumption that the consecutive moves of an individual are independent of each other (Swihart and Slade 1985). We might consider that *C. sordidus* met this assumption because the distribution of distances moved depended on numerous local random characteristics of soil, e.g., sinuosity of travel path. Moreover, this distribution was well predicted by the habitat-dependent model. The walks of other species, however, are more correlated, i.e., consecutive moves are related to each other (Patterson et al. 2008). A possible way to account for this dependence would be to consider the probability distribution of the angles defined by all the sets of three last positions of individuals, and computing for each cell c the turning preference θ_c according to this distribution. We could modify Eq.1 of the model by multiplying the relative preference α_c by the turning preference θ_c .

Likelihood comparisons and the POM framework have the same objective of increasing the understanding of the ecological process under study, but the approaches are different. Likelihood comparisons indicate which statistical model best describes the observed data. The POM framework, in contrast, indicates which mechanistic model fails to reproduce an observed pattern. Likelihood comparisons and POM are rarely used by the same community of scientists (Vinatier et al. 2010b) because the complexity and noise generated by the stochasticity of mechanistic models are hard to analyse with statistical methods (Grimm and Railsback 2005). In our study, the dispersal model chosen was simple enough to be tractable by likelihood comparisons and complex enough to allow the emergence of properties of space use at the population level. The complementarity between likelihood comparisons and POM was clearly demonstrated in our study.

Appendix A. Characteristics of the radio-tracking data set.

Study site

Studies were conducted in Martinique, French West Indies, where banana is the main cultivated plant. Climate is tropical, with temperatures ranging from 25 to 27°C and hygrometry from 70 to 80% during the study.

Habitat mapping

Banana plantations are composed of a matrix of heterogeneous habitats likely to influence *Cosmopolites sordidus* movements. Banana plants are considered as semi-perennial because plants are successively replaced by suckers emerging at irregular intervals from the lateral shoots of the mother plant, leading to almost 10 cropping cycles before destruction of the field. Each host plant is a mat consisting of a mother plant, a shoot, and an old plant. At the end of the first cropping cycle, banana leaves and other crop residues are cut and form a permanent litter cover on the soil. Ditches about 80 cm deep are formed to increase drainage. To characterize the environment of each plot, we considered that each plot consisted of a raster grid of 1-m x 1-m cells with the value of each cell representing the most common habitat in the cell (Fig. A1).

Radio-tracking data set

Adults of *C. sordidus* were trapped in the field near their release site. They were sexed and marked using passive RFID (radio-frequency identification) tags. A preliminary study in controlled conditions indicated that tags did not affect adult movement. After the adults were released in the plots, their positions were checked daily with a recapture rate ranging from 50 to 80% and a precision of the position of 30 cm (for more details on the procedure, see Vinatier et al. 2010a). *C. sordidus* movement is highly variable between individuals and between days, and ranges from 0 to 900 cm in one night. We extracted only relocations separated by 1 day and during the first week for analysis. This led to 3388 pairs of radio-tracking locations (Table A1). Locations defined in decimetres were rounded to the proximate meter in order to have each position located in the centre of a given cell of the raster grid.

Table A1.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Localisation	14°37'N, 60°58'W	14°37'N, 60°58'W	14°37'N, 60°58'W	14°37'N, 60°58'W	14°39'N, 60°58'W
Area	800 m ²	1600 m ²	1300 m ²	1300 m ²	2400 m ²
Period of study	September 2009	December 2009	July 2009	May 2009	January 2009
Effective length of study	8 days	11 days	29 days	22 days	38 days
Number of released weevils	261	144	360	360	204
Number of consecutive recaptures	544	228	1071	572	973

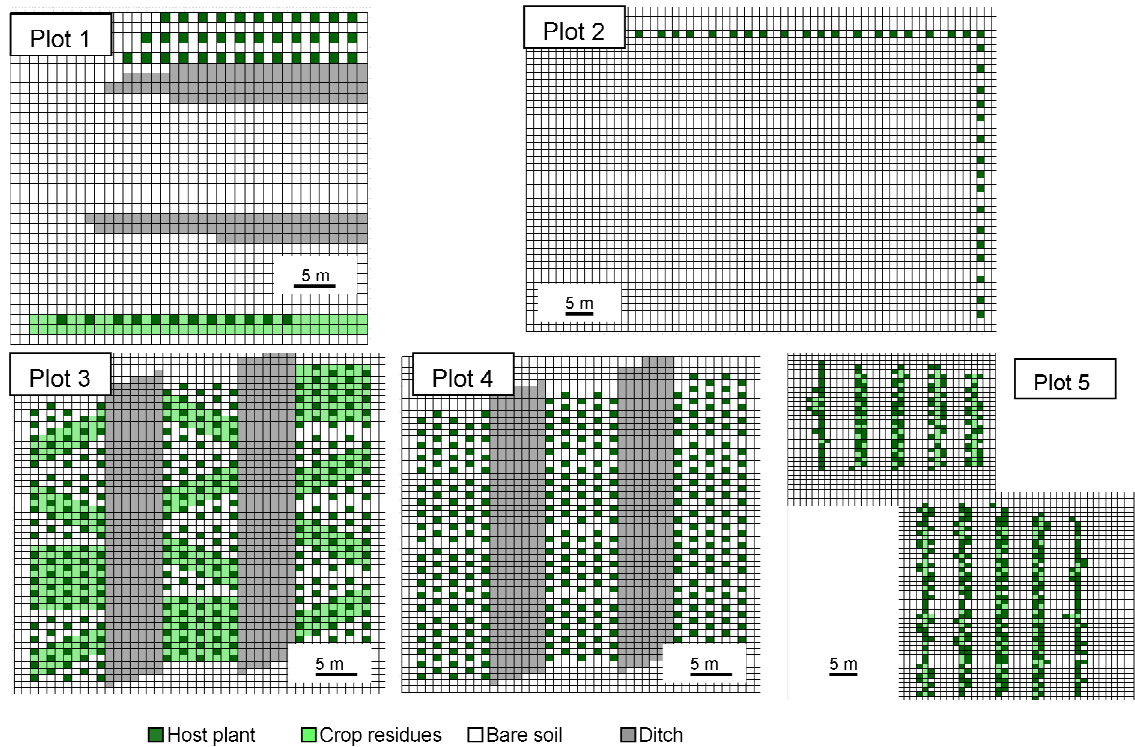


Figure A1. Plot-raster of the five habitats used for the *Cosmopolites sordidus* movement study. Each cell is a 1-m² square. Plots 1 and 2 are composed mainly of bare soil. The proportions of host plant and crop residues are larger in Plots 3-5 than in Plots 1-2. Host plants are planted in staggered rows in Plots 3 and 4, with a cover of crop residues in Plot 3. In Plot 5, host plants are planted in 10 irregular double-rows, with an irregular cover of crop residues between host plants in each double-row.

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CHAPITRE V – MISE AU POINT D'UN MODELE INDIVIDU CENTRE SIMULANT LA DYNAMIQUE SPATIALE DU CHARANÇON ET DE SES DEGATS

Fécondité, mortalité et dispersion sont les composantes principales de la dynamique d'infestation d'un bioagresseur. Il est nécessaire d'évaluer, dans notre cas d'étude, quelle est la part de chacun de ces processus dans la dynamique spatio-temporelle des attaques du charançon sur le long terme. Ces processus, trop complexes pour être analysés de manière analytique, nécessitent d'être intégrés dans des modèles mécanistes spatiaux. A l'heure actuelle, aucun modèle n'existe sur *C. sordidus*, et parmi les modèles spatiaux existants (cf. Chapitre II), les modèles individu-centrés s'avèrent les plus intéressants pour rendre compte des schémas de plantation de bananiers et des comportements de déplacement des individus.

Ce chapitre repose sur l'article publié dans *Ecological Modelling* et intitulé **COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields**. L'objectif est double:

- synthétiser et évaluer la pertinence des données bibliographiques existant sur le charançon dans l'optique de développer un modèle individu-centré sur cette espèce;
- tester à l'aide du modèle comment la plantation des parcelles de bananiers influe sur la dynamique spatiale et temporelle des infestations de charançon.

Le modèle COSMOS a été implémenté à partir des données bibliographiques existantes et évalué à l'échelle d'une micro-parcelle de bananiers (**Figure V-1**). Le développement de sa plante-hôte, le développement et la mortalité des stades préimaginaux, la longévité et la fécondité des adultes ont été intégrés au modèle. L'analyse de sensibilité des paramètres du modèle selon la méthode de Morris a révélé l'importance de la longévité et de la fécondité sur la variabilité et l'intensité des attaques. La confrontation des résultats de simulation aux données réelles, rarement rencontrée en modélisation individu-centrée, fait l'originalité du manuscrit.

Les résultats de l'expérience de télémétrie (Chapitre III) ont été connus **après** l'implémentation du modèle COSMOS et sa publication, par conséquent le processus de déplacement de cette version du modèle était basé sur les données de la littérature (Delattre 1980). Il a donc été nécessaire de vérifier que les résultats trouvés avec l'ancienne version du modèle COSMOS demeuraient valable avec le modèle programmé selon la nouvelle fonction de déplacement (**Annexe B**).

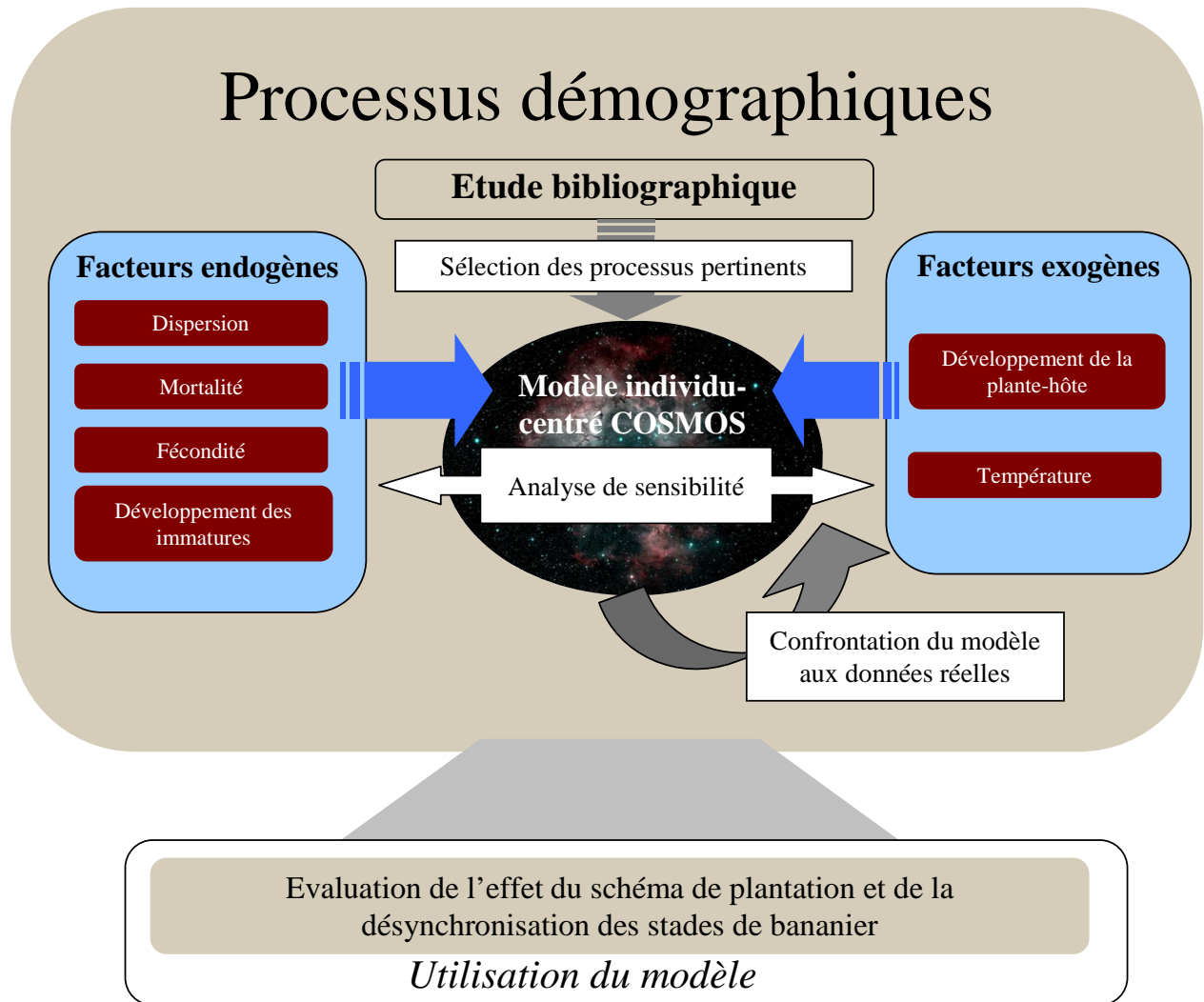


Figure V-1. Schéma de la démarche de compréhension des processus démographiques agissant sur l'infestation du charançon du bananier.

COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields.

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Abstract

A stochastic individual-based model called COSMOS was developed to simulate the epidemiology of banana weevil *Cosmopolites sordidus*, a major pest of banana fields. The model is based on simple rules of local movement of adults, egg laying of females, development and mortality, and infestation of larvae inside the banana plants. The biological parameters were estimated from the literature, and the model was validated at the small-plot scale. Simulated and observed distributions of attacks were similar except for five plots out of 18, using a Kolmogorov-Smirnov test. These exceptions may be explained by variation in predation of eggs and measurement error. An exhaustive sensitivity analysis using the Morris method showed that predation rate of eggs, demographic parameters of adults and mortality rate of larvae were the most influential parameters. COSMOS was therefore used to test different spatial arrangements of banana plants on the epidemiology of *C. sordidus*. Planting bananas in groups increased the time required to colonise plots but also the percentage of banana plants with severe attacks. Spatial heterogeneity of banana stages had no effect on

time required to colonise plots but increased the mean level of attacks. Our model helps explain key factors of population dynamics and the epidemiology of this tropical pest.

Keywords: Banana weevil; Curculionidae; Individual-based model; Life-history traits; *Musa*; Spatially Explicit Model; West Indies

1. Introduction

Understanding the epidemiology of pests is of special importance for better management (Zadoks and Schein, 1979; Madden, 2006). The spatial component of epidemiology is a crucial element in the spread of damages from a localised inoculum or when pest dispersal is limited (Winkler and Heinken, 2007). Fecundity, mortality, and dispersal are the driving forces of insect epidemiology (Schowalter, 2006, p. 137). Pests can disperse heterogeneously (Lopes et al., 2007). The dispersal behaviour of mobile stages between each host plant contributes greatly to explaining variations of local densities of the species (Coombs and Rodriguez, 2007). In tropical and subtropical regions, where populations of plants and pests are not synchronised by severe winters, all stages of most insects are present simultaneously (Godfray and Hassell, 1987). In these conditions, all stages should be considered simultaneously to understand the distribution and abundance of organisms in the field. This approach is different from the ones in temperate regions, which focus on a particular part of the life cycle of insects that is considered as a key point of spatial patterning and demography, such as attacks or dispersal behaviour of adults (e.g. Cain, 1985; Brewster et al., 1997), egg laying of females (Zu Dohna, 2006), or post-embryonic stages (egg or larva) (e.g. Johnson et al., 2007).

In this work, we took as case study the banana weevil *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar. 1825), a major pest of banana cropping systems. Larvae bore into the corm of banana plants and damage the points of insertion of primary roots, leading to plant snapping and toppling (Montellano, 1954; Gold et al., 2001). *C. sordidus* can contaminate new banana plantations through infested planting material or by means of adults that have survived since the last banana planting, because it has a long development time and life span, a low mortality rate, and is able to survive without food for extended periods (2-6 months) in moist environments (Gold et al., 2001). Adult weevils, which have limited

dispersal abilities, can also invade new plantations from nearby plantations or from fallows when heavily infested banana plots are transformed into fallows (Gold et al., 2001). Banana plant stages may be heterogeneous in a plot, because plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner, 1994). This spatial heterogeneity of banana plant stages is likely to influence weevil population dynamics because of the influence of banana stage on female egg laying (Cuillé, 1950; Vilardebo, 1973). Based on these characteristics, we chose (i) a spatially explicit approach to understand how local movements influence the spatial distribution and damages of this pest in relation to its habitat and (ii) an individual-based modeling (IBM) approach to help explain observed population patterns (Winkler and Heinken, 2007), considering that different behaviours at the individual level can lead to the emergence of population-level properties (Grimm and Railsback, 2005). Modeling was considered as a good means to implement these approaches and an IBM was chosen as the modeling framework.

In this paper, we present the COSMOS model, aimed at simulating the spatial epidemiology of *C. sordidus* in the long-term by describing its population dynamics and the resulting infestation of host plants. The model considers all insect stages simultaneously and assumes there are individual variations in behaviour according to each developmental stage. We hypothesised that the distribution of *C. sordidus* populations and attacks in banana fields can be modelled according to epidemiological rules identified at an individual level and calibrated from the literature, with a model that is less parameter-demanding than most IBMs. The COSMOS model, like many IBMs, aims at bridging the gap between individual behavioural ecology and population dynamics (De Angelis and Gross, 1992). We validated COSMOS by comparing model outputs with field data, which is rarely done with most IBMs (Alderman

and Hinsley, 2007; Charnell, 2008). Then, because sensitivity analyses are key steps of the modelling processes (Parry et al., 2006; Arrignon et al., 2007), we first conducted an exhaustive sensitivity analysis using the Morris method (Morris, 1991) to identify the most influential parameters in our model. In a second step, these parameters were studied in detail on an extended range of variation, including extreme values. Finally, we used COSMOS to test how planting patterns and the spatial heterogeneity of plant stages, resulting from the variability of sucker appearance over cropping cycles, could modify the time necessary to colonise the whole plot and the level of damage during three cropping cycles, when the initial weevil population was distributed along one side of the plantation.

2. Model description and parameterisation

2.1. General features of the COSMOS model

The COSMOS model is a stochastic IBM that runs on a daily time step. It simulates the local movement and egg laying of females in the field, infestation of larvae in banana plants, and the main features of insect and host plant development (**Figure V-2**). According to the model, individual *C. sordidus* disperse in a field that is represented by a grid with one banana plant per cell (grid area ranged between 144 and 441 m²). Plants pass through three distinct stages until harvest: maiden sucker, preflowering, post-flowering. Just before flowering, a new sucker of the mother plant is selected that grows simultaneously in the same cell. The time lag between two consecutive harvests, corresponding to a cropping cycle, is about 200 days (see Tixier et al. (2004) for details on banana cropping cycles).

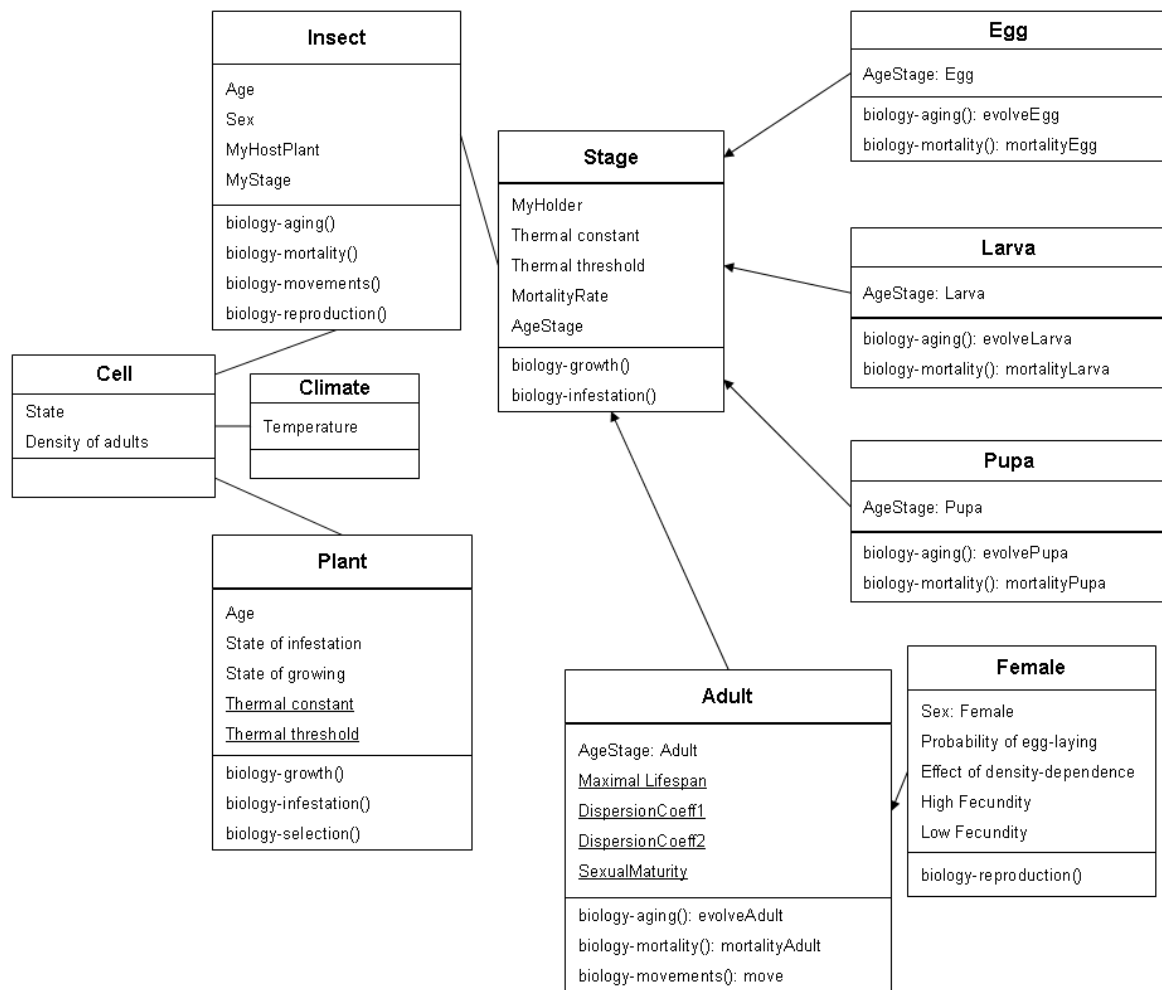


Figure V-2. Static structure of the spatially explicit model COSMOS in Unified Modeling Language (UML). Each box contains the name of a class in the first part, its key attributes in the second part, and the rules in the third part. For example, an individual of class Adult moves according to the rule biology-movements () and the key attributes DispersionCoeff1 and DispersionCoeff2. Class attributes are shared for all the individuals of the class (underlined names) and instance attributes have a specific value for each instance (non-underlined names). Arrows between boxes signify inheritance, and simple links signify association. For example, an individual of class Adult inherits from class Stage and is associated with class Insect.

C. sordidus females lay eggs on banana plants, and larvae issued from these eggs bore into the corm of the plants. The stage duration of juveniles and the phenologic stages of banana plants are temperature-dependent. In the COSMOS model, each *C. sordidus* is an autonomous individual that has a set of rules for egg laying and movement behaviour, depending on the plant stage at the insect's current position. Males do not cause damage, and no data are available on the influence of mating on egg laying. Therefore, males were excluded from the model.

A rule is an algorithm specified by the modeller to define a behaviour of individuals (Grimm and Railsback, 2005). The platform used to develop the model was the CORMAS (Common-pool Resource and Multi-Agents System) software (Bousquet et al. (1998); see <http://cormas.cirad.fr>), which is based on the Smalltalk object-oriented language (Visual Works 7.5, Cincom Softwares). The architecture of the model was developed in accordance with Ginot et al. (2002). **Table V-1** presents all the model parameters described below and their estimated values.

2.2. Dispersion

Eggs, larvae, and pupae cannot disperse between banana plants, and adults disperse slowly by crawling (Gold et al., 2001). Although the banana weevil has functional wings, most observers have reported that the weevil seldom, if ever, flies (Gold et al., 2001). In banana fields planted in monoculture (1500 to 2200 plants/ha, with standard planting distances of 2.4×2.4 m), individuals do not search for food in a large area; their behaviour rather corresponds to an area-restricted search response type (Morris and Kareiva, 1991). The proportion of individuals that disperse to a given banana plant can be estimated as a negative exponential function of the distance to the plant (Schowalter, 2006). Adjusting the data of Delattre (1980) and Gold et al. (2001) to such a function, the probability (P) each time step of an adult moving to a given banana plant at distance d (in m) is the following (**Eq. (1)**):

$$P=0,06 e^{-0,62 d}$$

(1)

2.3. Egg laying and longevity of adults

Once inseminated, *C. sordidus* females can stay gravid for 15 months without renewed mating (Cuillé, 1950; Treverrow et al., 1992). Authors disagree on the possible effect of age on egg laying (Gold et al., 2001). Yet it is agreed that egg laying depends mainly on two processes. First, egg laying probability and fecundity increase over banana phenologic stages (Cuillé, 1950; Vilardebo, 1973); the maximal probability of egg laying and fecundity occurs at the post-flowering stage, see **Table V-1** (Koppenhofer, 1993; Abera et al., 1999). Second, egg laying activity declines when the number of adults per plant increases (Cuillé, 1950; Koppenhofer, 1993; Abera et al., 1999).

In our model, mating and the effect of age on egg laying are not considered. Egg laying occurs for each female once a week, according to the period found in the literature (Koppenhofer, 1993), and follows a binomial distribution with a probability depending on the stage of the host plant (flowering, preflowering and maiden sucker) as estimated by Abera et al. (1999). If conditions for egg laying are fulfilled, the fecundity of each female is assumed to be Poisson-distributed (in accordance with Hilker et al. (2006)), with parameter equal to 2.7 if the adult density exceeds a given threshold (*DE*, **Table V-1**) and 0.8 otherwise.

The maximal lifespan of adult of *C. sordidus* was estimated to be 748 days (Froggatt, 1925; Gold et al., 2001). The mortality rate of adults is often considered as constant during their lifespan (Godfray and Hassell, 1989; Berec, 2002; Potting et al., 2005). To our knowledge, no data are available on the predation rate of *C. sordidus* adults in the field.

Following Bousquet et al. (2001), *MR* was calculated assuming a discrete decreasing process, as a function of the maximum lifespan (*ML*, in days, **Table V-1; Eq. (2)**). We assumed a high

mortality rate (0.99) of adults from emergence to the maximum lifespan and a constant daily mortality (MR). The shape of the survival schedule exponentially decreases in those conditions and is convex (Carey, 2001).

$$MR=1-(0.01)^{1/ML} \quad (2)$$

2.4. Development and mortality of immature stages

The development of *C. sordidus* is driven by temperature (Kiggundu et al., 2003a). Eggs, larvae, and pupae have different intrinsic mortality rates; larvae are the most susceptible stage (Traore et al., 1993; Traore et al., 1996; Kiggundu et al., 2003b). However, eggs laid on the surface of the corm are exposed to additional mortality by predators, e.g. ants (Koppenhofer, 1993; Abera-Kalibata et al., 2007; Abera-Kalibata et al., 2008). Mortality rates of immatures and additional mortality resulting from predators are shown in **Table V-1**.

In the model, the physiological age for each juvenile stage i increases each day, at a rate determined by the difference between the daily temperature and a thermal threshold corresponding to stage i . Daily temperature was calculated as the mean between minimum and maximum temperature. **Table V-1** presents the thermal constants, i.e. the number of degree-days above the thermal threshold required to complete development from stage i to the $i+1$ th stage. Mortality at stage i follows a binomial distribution based on a constant mortality rate, because the literature gives only cumulative mortality rates at the end of each stage.

2.5. Development of banana plants

The thermal threshold for banana-plant development was estimated to be 14°C (Ganry, 1980), and the duration in degree-days of each stage from planting to harvesting was determined by Abera (1997) and Tixier et al. (2004) (**Table V-1**). In the COSMOS model, flowering rate follows a normal distribution (mean = 2350 degree-days; σ = 200 degree-days), adapted from

Tixier et al. (2004). The sucker of the following cycle is selected after 2180 degree-days (Tixier et al., 2004).

2.6. Infestation of banana plants

Damage resulting from adult *C. sordidus* feeding is negligible compared to that resulting from larvae (Gold et al., 2001). When larvae are ready to pupate, they burrow toward the outer surface of the corm (Froggatt, 1925). The attacked circumference (AC), measured at the outer surface of the corm of each banana plant, is a common indicator of damage; it is assumed to be proportional to the number of galleries bored by the larvae. When the whole circumference of the corm is attacked, eggs and larvae die because of resource limitation (Koppenhofer and Seshu Reddy, 1994).

In the model, at each time step, the attacked circumference (AC) is estimated as the total number of larvae that have reached emergence multiplied by the mean diameter of a gallery (i.e. 1 cm according to Montellano (1954) and Sponagel et al. (1995)). The maximum value of AC is equal to the maximum circumference of the banana plant at harvest.

Table V-1. Model parameters, their values and ranges for sensitivity analyses, and corresponding references.

Description	Code	Value	Range used for the first sensitivity analysis	References
Egg				
Thermal constant to reach next stage (degree-days)	TCE	89	80.1-97.9	(Gold et al., 2001)
Thermal threshold for development (°C)	TTE	12	10.8-13.2	(Gold et al., 2001)
Mortality rate for eggs	MRE	0.11	0.09-0.12	(Kiggundu et al., 2003)
Proportion of eggs removed by predators	PE	0.6	0.33-0.68	(Koppenhofer, 1993; Abera-Kalibata et al., 2008)
Larva				
Thermal constant to reach next stage (degree-days)	TCL	537.9	484.1-591.7	(Traore et al., 1996)
Thermal threshold for development (°C)	TTL	8.8	7.9-9.7	(Traore et al., 1996)
Mortality rate for larvae	MRL	0.48	0.32-0.64	(Kiggundu et al., 2003)
Diameter of gallery (in cm)	G	1	0.8-1.2	(Montellano, 1954; Sponagel et al., 1995)
Pupa				
Thermal constant to reach next stage (degree-days)	TCP	120.7	108.6-132.8	(Traore et al., 1996)
Thermal threshold for development (°C)	TTP	10.1	9.09-11.11	(Traore et al., 1996)
Mortality rate for pupae	MRP	0.18	0.095-0.265	(Traore et al., 1996)
Adult				
Sex-ratio (male:female)	-	1:1	-	(Gold et al., 2001)
Sexual maturity for females after emergence (days)	SM	34.5	33-36	(Cuillé, 1950)
Probability of egg-laying on Maiden Sucker compared to Flowered plants	OPMS	0.11	0.08-0.13	Estimated from Abera (1997)
Probability of egg-laying on Preflowered plants compared to Flowered plants	OPPF	0.41	0.39-0.46	Estimated from Abera (1997)
Number of adults per week necessary for density-dependent effect on fecundity	DE	20	10-33	(Abera, 1997)
Number of eggs per week per female without density-dependent effect	FH	2.7	1.7-3.2	(Koppenhofer, 1993)
Number of eggs per week per female with density-dependent effect	FL	0.8	0.6-1.1	(Koppenhofer, 1993)
Proportion of individuals moving 2 meters per time step (%)	DC1	1.4	1.5-6.6	(Delattre, 1980)
Proportion of individuals moving 4 meters per time step (%)	DC2	0.3	0.0-3.0	(Delattre, 1980)
Maximum lifespan of adult (days)	ML	748	520-900	Estimated from Froggatt (1925)
Banana plant				
Interval planting-maiden sucker (degree-days)	-----	800	-----	Estimated from Abera (1997)
Interval planting-preflowering (degree-days)		1600		Estimated from Abera (1997)
Interval planting-post-flowering (degree-days)		2350		(Tixier et al., 2004)
Standard deviation for flowering rate (degree-days)		200		Adapted from Tixier et al.(2004)
Appearance of first sucker (degree-days)		2180		(Tixier et al., 2004)
Interval planting-harvesting (degree-days)		3250		(Tixier et al., 2004)
Thermal threshold (°C)		14		(Ganry, 1980)
Maximal circumference of plant at harvesting (cm)		60		

3. Material and methods

3.1. Field data

Damages of *C. sordidus* on banana plants were measured on 18 plots during two cropping cycles at the CIRAD experimental station, Neufchâteau, Guadeloupe (French West Indies, 16°15'N, 61°32'W, altitude 250 m) between 1990 and 1995. The plots contained 30-42 banana plants (2174 plants/ha, *Musa* spp., AAA group cv. Cavendish Grande Naine) and were separated by a row without plants. Initial inoculums of *C. sordidus* arrived from previous banana crops. At each harvest, damages caused by larvae inside the corm were evaluated on each banana plant by removing 10 cm of topsoil around the corm and a band of tissue 7 cm wide and 0.5 cm deep across the corm at its widest point. The circumference of the corm with galleries was measured using a tape measure.

3.2. Simulation procedures

Model validation

The simulation area was a 15×15 to 18×21 cell grid (cell dimension: 0.8×0.8 m), according to the number of banana plants in each field. Each banana plant belonged to one cell and was separated from other plants by two empty cells. Simulations were run over 200 days, corresponding to the period between two consecutive harvests. Model inputs consisted of daily mean temperature from a five-year dataset and of initial populations (see below). Because of the model stochasticity, we performed 100 replicates for each situation and averaged the results.

For each of the 18 plots used for model validation, the model was initialised using populations of individuals distributed in the plot, estimated according to the attacks recorded at the end of the first cycle for each plant, i.e. the attacked circumference (AC). For this estimation, we first

established a relation to calculate the number of adults per plant from AC using data from a capture-recapture study performed in a banana field in Neufchâteau (1996-1997). In this study, populations had been trapped using pseudostem traps (Gold et al., 2002), and AC had been measured for each banana plant. The ratio of the abundance of *C. sordidus* adults (square-root-transformed to stabilise the variance) to AC was 0.22 ± 0.07 ($F= 18.85$; $P<0.01$; $df= 50$). Having calculated the number of adults at the end of the first cropping cycle in each cell of the 18 grids by using this ratio, we set the population age structure, using ratios of 0.24, 0.48, 0.10, and 0.18 for egg, larvae, pupae, and adults, respectively (Koppenhofer, 1993). Within each stage the age was considered to follow a uniform distribution. Then, the model simulated the epidemiology of *C. sordidus* during the second cropping cycle.

Simulation of spatial arrangements of banana plants

We simulated different spatial arrangements of banana plants thought to have an effect on the time necessary for *C. sordidus* to colonise a plot and to cause damage. First, we simulated three planting patterns with synchronous banana stages (**Figure V-3**): (1) regular planting (2.4×2.4 m), (2) double row planting (0.8 or 4×2.4 m) and (3) patches of nine banana plants (5.6×5.6 m between each patch). The age of banana plants at initialisation was one month. Then, we simulated a regular planting pattern with asynchronous banana plant stages (4; **Figure V-3**), i.e with different stages of plants in the same plot at the same time. In pattern 4, plant stages were randomly set from one month (planting) to nine months (harvest); this situation is representative of old banana plots, which are unsynchronised because of the common practice of repeated sucker selection (Tixier et al., 2004; Lassoudière, 2007). For all patterns, 81 banana plants were distributed over a grid of 27×27 cells with a cell size of 0.8×0.8 m, yielding a planting density of 1750 plants/ha.

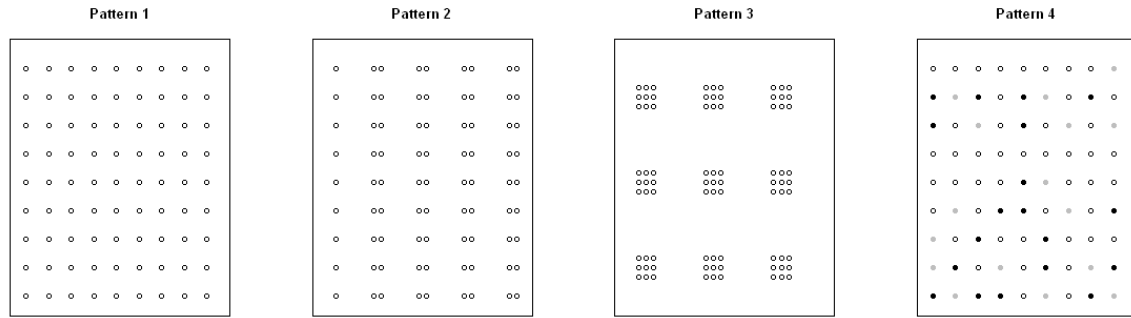


Figure V-3. Spatial arrangements of banana plants used in simulations: regular planting (1), double row planting (2), patch planting (3), regular planting with heterogeneity of banana stages (4). Color gradation figures from white to black the different banana stages from the youngest to the oldest, respectively. Planting density is 1750 plants/ha everywhere.

At initialisation, different populations of adults of random age were equally distributed over the first column of the grid, representing the beginning of a rapid invasion due to putting an infested plot in fallow near the tested grid. For each pattern, we computed the time necessary for at least one adult to reach the column on the opposite side of the grid, the time-series of the mean intensity of attacks of each plant (AC), and the time-series of the percentage of plants with severe attacks (more than 20 cm of AC) over the entire period of simulation (600 days). Boundaries of grid were closed. Top and bottom edges represented a barrier; left edge the source of contamination that is unidirectional. As simulation stopped when one adult reached the last column of the grid, effect of right edge is absent. This experimental design allowed low edge effects, based on an infestation from one side to the other.

3.3. Sensitivity analyses

In a first step, we used the Morris method (Morris, 1991; Cariboni et al., 2007; see **Appendix A**) to discriminate the model parameters having the highest influence on the variability of mean and standard deviation of attacks, on four plots with different level of attacks (Plots 8, 9,

10 and 16). Two ranges of parameter values were defined for this analysis, the first one corresponding to the uncertainty of estimates according to the literature, the other equally proportioned from -20% to 20% of the value in **Table V-1**. Parameters equally discriminated using the two ranges were considered as the most influential.

In a second step, the parameters that were the most influential according to the first discrimination were tested one by one using a simple sensitivity analysis, the other parameter values being held constant. The model outputs were as before the variability of mean and standard deviation of attacks. For each parameter, different ranges of values were set, from 0 to 1 for biological rates and from 0 to an extreme value empirically defined (when model outputs no longer responded to parameter variations) for the other parameters. For each parameter value, 100 simulations were performed and the results arranged as boxplots showing the quartiles of the output distribution (Arrignon et al., 2007). For all the sensitivity analyses, plot 8 was chosen as representative of the studied plots, after examination of the first simulations (data not shown).

3.4. Statistical methods

For each plot used for model validation, smoothed distributions of the simulated attacks were plotted using 100 replicates of each simulation and compared with observations; this smoothing method is issued from Sheater and Jones (1991). Plotting smoothed distributions instead of histograms allow a better comparison between simulations and observations. The average distribution of the simulated attacks was compared to the observed attacks for each plot using the Kolmogorov-Smirnov (ks) test (Mellin et al., 2006). If the value of the probability associated to the ks test is greater than the level of significance (commonly 0.05), the null hypothesis of conformity (similar distributions) cannot be rejected. For each plot, the simulated mean and standard deviation of the distribution of attacks were compared to the

observations over 100 replicates. The mean difference between observation and simulation was calculated using the RMSE (root mean squared error (Wallach and Goffinet, 1989)).

All statistical analyses were performed with the R software (R_Development_Core_Team, 2008) using basic packages: “lattice” (for plotting the distributions of attacks using the kernel density estimate) and “sensitivity” (for sensitivity analysis using the Morris method).

4. Results

4.1. Model validation

Figure V-4 shows a good agreement between observed and simulated smoothed distributions of attacks for most plots. However, observed and simulated distributions were different for Plots 2, 4, 6, 9, and 17 according to the Kolmogorov-Smirnov test ($P < 0.05$). For Plots 2, 4, and 6, the model overestimated the frequency of high levels of attacks while it underestimated low levels of attacks (**Figure V-5**). For these plots, mean observed and simulated attack circumference (AC) were 10-15 cm and 25-30 cm, respectively. For Plots 9 and 17, the model could not simulate the bimodal distribution of observed attacks. The model predicted well when the level of attacks at initialisation was relatively low (e.g. on Plots 16 and 18, where the mean observed AC was 0 and 2 cm, respectively); and relatively high (Plots 1, 11, 14, where the observed AC was 23 to 25 cm). The RMSE between the observed and simulated mean AC of the 18 plots was 7.7 cm; it improved when excluding plots 2, 4, and 6 (3.7 cm). The RMSE of the standard deviation was 2.6 cm for the 18 plots.

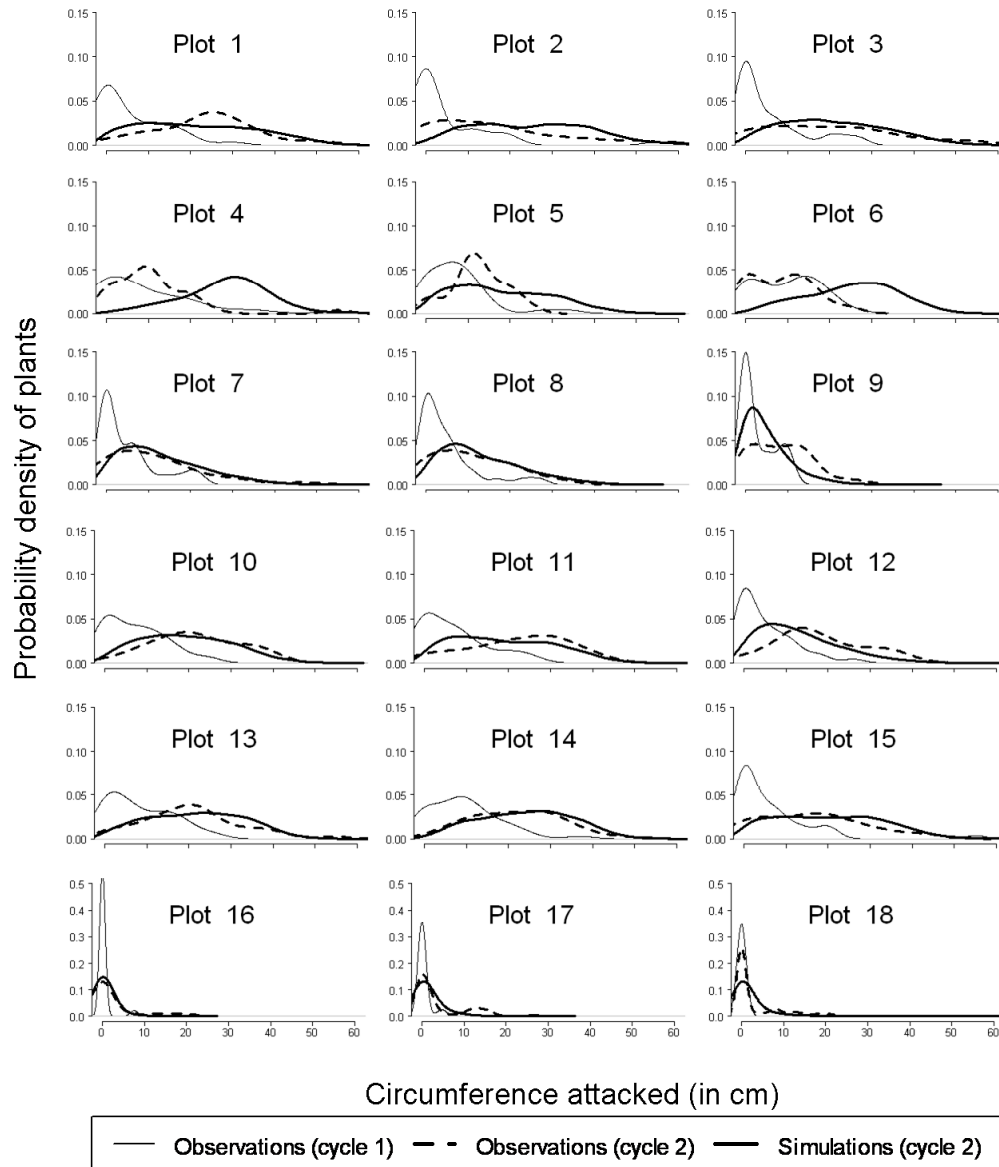


Figure V-4. Observed and simulated distribution of banana damages in 18 plots infested by *C. sordidus* in Guadeloupe. Distributions are depicted by probability densities. Simulated probability densities were obtained over 100 runs for each plot. The solid thin line represents the distribution of attacks at the end of the first cycle (initialization). Bold lines represent the observed (dotted) and simulated (solid) distributions. Note that y-scale are different for Plots 16-17-18.

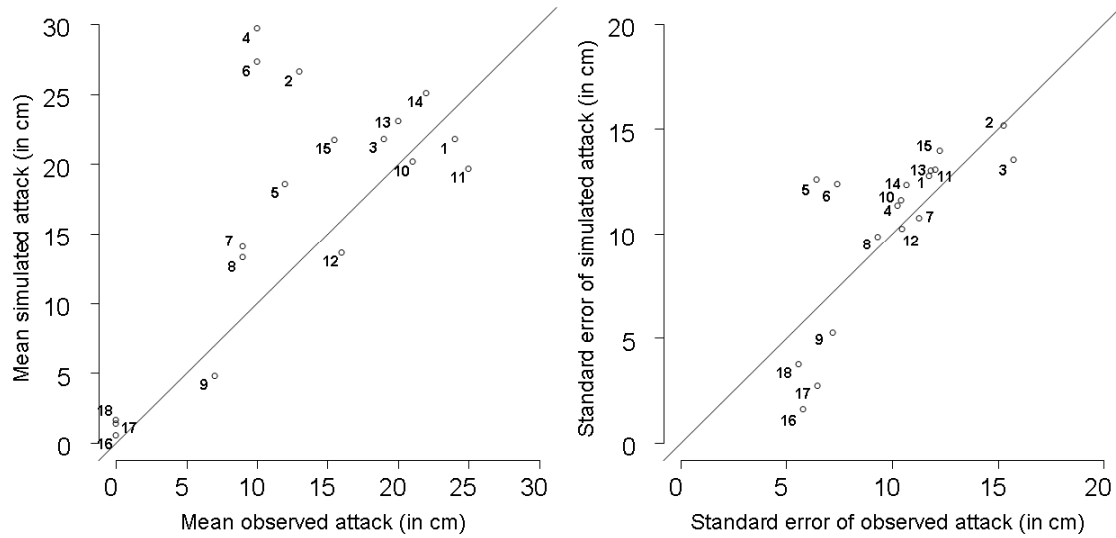


Figure V-5. Comparison of observed vs simulated (a) mean and (b) standard deviation of distributions for each plot. Solid line indicates a perfect fit between observation and simulation. Numbers correspond to Plot numbers.

4.2. Sensitivity analysis

The Morris method showed that six parameters had a major influence on mean and standard deviation of the distribution of attacks: *DE*, *FH*, *ML*, *MRL*, *PE* (demographic parameters), and *G* (diameter of gallery; **Appendix A, Table V-1**). Since the six parameters were similarly highlighted for the four tested plots, only the results for plot 8 were showed in **Appendix A**. *PE*, *MRL*, *G* and *FH* had a greater influence than *DE* and *ML*. On an extended range of variation, the increase in *PE* and *MRL* linearly decreased the mean level of attacks. The influence of *FH* (female fecundity) on the standard deviation of attacks decreased for more than eight eggs per week. For increasing values of *FH*, *DE*, *G*, and *ML*, the mean values of attacks increased linearly and then plateaued (**Figure V-6**).

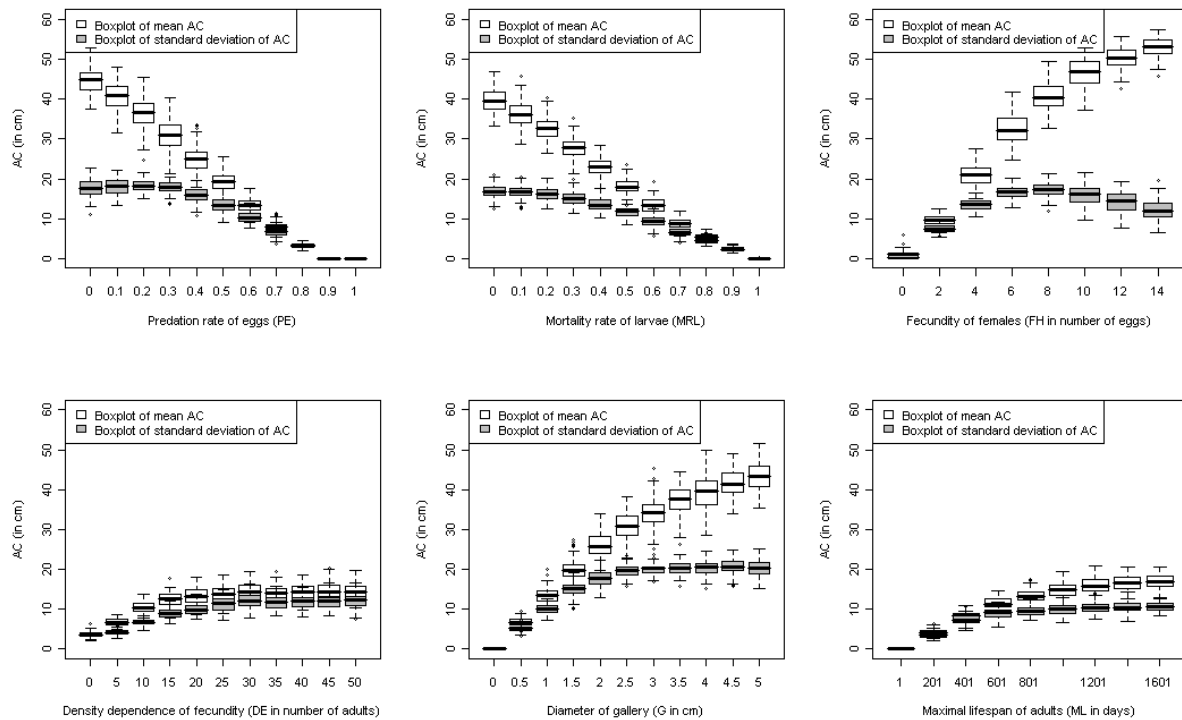


Figure V-6. Analyses of the COSMOS model sensitivity to the most influent insect biological parameters, focusing on two main parameters of the distribution of attacks on plot 8: mean (white boxes), standard deviation (grey boxes). A range of values was tested for each parameter, the other parameters being held constant. The output of 100 runs was computed in a boxplot. Each boxplot contains the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker. The whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box.

4.3. Simulated effect of spatial arrangements of banana plants

The time necessary to cross the field was considerably higher for pattern 3 than for the other patterns, while a shorter time was found for pattern 4 (**Table V-2**). This result remained the same when the initial population varied; times were reduced by half when the population varied from 50-400 individuals (data not shown). Mean levels of attacks at 300 days (harvest of first cycle) and 500 days (harvest of second cycle) were similar for planting patterns 1, 2 and 3 and twice as high for pattern 4.

Table V-2 Time to cross the plot and mean level of attacks at 300 and 500 time steps for the 4 spatial arrangements of banana plants illustrated in **Figure V-7** (initial population : 50 adults).

	Time to cross the plot (in days) \pm SE	Mean AC at 300 days (in cm) \pm SE	Mean AC at 500 days (in cm) \pm SE
Pattern 1	184 \pm 8	2.44 \pm 0.08	6.89 \pm 0.3
Pattern 2	197 \pm 8	2.41 \pm 0.09	7.03 \pm 0.2
Pattern 3	395 \pm 14	2.55 \pm 0.08	7.47 \pm 0.3
Pattern 4	170 \pm 7	6.22 \pm 0.16	16.24 \pm 0.46

Figure V-7 shows that the mean level of attacks increased to a higher level for pattern 4 than for patterns 1, 2, and 3. For patterns 1, 2, and 3, we observed a small inflexion of the mean level of attacks between 300-350 days and 500-550 days after planting (**Figure V-7a**). The percentage of plants with severe attacks ($AC > 20$ cm) increased faster for planting pattern 4, followed by patterns 3, 2, and 1 (**Figure V-7b**).

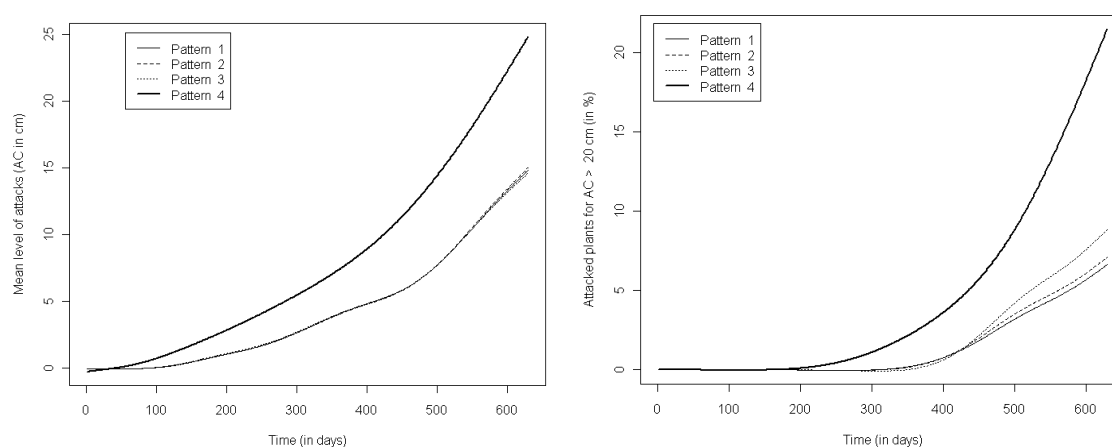


Figure V-7. Evolution of the mean intensity of attacks (a) and percentage of severe attacks (AC greater than 20 cm) (b), resulting from *C. sordidus* infestation of a plot. Initialization of the model was done for 50 individuals at one side of the plot, figuring a massive infestation from a neighboring field.

5. Discussion and conclusion

The individual-based COSMOS model accurately predicted the distributions of attacks of *C. sordidus* on banana plants for 13 out of 18 plots. This quality of prediction is attested for a

large range of initial levels of attacks. The RMSE value of mean attacked circumference (7.7 cm) may be the consequence of overestimation of three validation plots and/or measurement error in the field. Furthermore, in the tested range of attacks, the standard deviation of the attacks in the plot was well maintained. Measurement error in the field could be due to an overlapping of some galleries in the same plant or to the presence of some galleries above or below the observation area. For three validation plots out of 18, the model overestimated the mean level of attacks. This overestimation could be explained by a greater predation of eggs in these plots than is accounted for by the model, predation of eggs being a major parameter according to the results of the sensitivity analyses. A highly variable density of *Pheidole* spp., a possible predator of *C. sordidus* eggs, was found among sites in a field trial in Uganda, ranging from 3.1-38.4 individuals per trap (Abera-Kalibata et al., 2008). Based on a recent survey in French West Indies, it seems that several species of ants are present in banana fields, including *Pheidole* spp. (Duyck P.-F., pers. com.).

COSMOS compiles almost all of the existing knowledge about the biology of *C. sordidus*, benefiting from many experimental studies (Gold et al., 2001 and references therein). Nevertheless, our sensitivity analyses highlight the importance of better specifying key biological parameters to improve predictions, such as egg predation, adult mortality, and density-dependent effects. The level of egg predation is a key factor but is variable (Abera-Kalibata et al., 2008), which calls for further investigations. As explained by Carey (2001), little is known about mortality and longevity of insects, whereas they are fundamental epidemiological processes. The effect of density dependency of egg laying is also an influential parameter (Cuillé, 1950; Koppenhofer, 1993; Abera et al., 1999), but further studies should explore the whole range in which density dependency is established. It is also important to fill the lack of available data on predation rate of adults in the field, following the

example of Sutherst et al.(2000) on ticks. For that purpose, field and laboratory experiments are currently conducted in French West Indies to identify the main predators of *C. sordidus*, and quantify their predation rates (P.-F. Duyck, pers.com.).

Our simulations on the effect of different spatial arrangements of banana plants on the epidemiology of *C. sordidus* show that planting in patches with a large distance between patches should limit the time necessary for the pest to colonise a new field. Indeed, in this case, only a small proportion of individuals is able to invade new patches. In contrast, the simulations indicate that the severity of attacks may increase when banana plants are planted in patches. Potting et al. (2005) in a modeling study on herbivores, found the same result, with a higher level of damages in patches than in rows. The pattern 3 figures patches with high concentration of plants. The hypothesis of resource concentration has been studied by Levine and Wetzler (1996). They have tested with an individual-based model the effect of planting decisions on attack frequencies by herbivorous insect pests, and they concluded that probability of host plant attack emerged partly as function of density of plants within patches. Furthermore, they estimate that probability of attack is function of radial distance detection of host by insect. In COSMOS, radial detection is defined by weak dispersal abilities of adults, as defined by literature. These weak abilities contribute also to increase intensity of attacks inside patches. Planting banana regularly or in double rows resulted in similar simulated colonisation time and intensity of attacks. This is probably because in the case of double row spacing, the slow spreading of *C. sordidus* in large interstices between rows was compensated by fast spreading in small interstices inside rows. Unsynchronised banana plantation decreased the time of colonization of the plot by *C. sordidus* and increased the severity of attacks. In this pattern, at every time step, *C. sordidus* can find stages of banana plant suitable for egg laying. In contrast for the other patterns, the inflexion of mean AC observed at t=300-

350 days and $t=500-550$ days may be explained by the lack of stages of banana plant suitable for egg laying after harvest. For management purposes at the landscape scale, farmers should avoid transforming a heavily infested field into fallow close to an unsynchronised field free of *C. sordidus*. At the field scale, planting in patches would limit the time of colonisation but after two or three cropping cycles, attacks might be severe. Such a strategy might be suitable for cropping systems with a limited number of cropping cycles. For cropping systems with more cropping cycles, regular and double row planting patterns of plantation would be more suitable.

The choice of the model type is governed by both spatial characteristics of habitat and insect traits. In a spatial insect model figuring infestation of melon by aphids, Lopes et al. (Lopes et al., in press) introduced space implicitly because they consider local movement as negligible. In that model, populations of aphids are described by partial differential equations, figuring the continuous development of populations. In our case, weak dispersal abilities of *C. sordidus* have required to introduce space explicitly. Populations of *C. sordidus* are described at individual level because of its discontinuous development and the presence of all stages with different behaviour at the same time. These results show that COSMOS is an interesting tool to design planting schemes for the control of banana weevil. IBM models have rarely been used for such purposes on pests. Generally, they have dealt with spatial heterogeneity as a means of controlling pests by simulating the incorporation of non-attractant crops in the field (Potting et al., 2005; Choi et al., 2006).

The basic principles of the epidemiology of *C. sordidus* were successfully integrated in the COSMOS model. Further steps in developing this model should consist of integrating more management practices able to influence the epidemiology of this pest and to contribute to

Integrated Pest Management (Huffaker and Gutierrez, 1999, p. 682), such as the use of resistant varieties, traps, and biological control agents, as suggested by Gold et al. (2001). This could be done by designing a sub-model that accounts for trapping. For this, existing algorithms (Byers, 1993; Branco et al., 2006) may be adapted to COSMOS. Furthermore, to design IPM schemes at the farm scale, the next step will be to upscale the model to a group of fields and to account for interfaces between fields.

The COSMOS model, by capturing the population trend of a tropical pest, is a powerful tool to analyse population processes of this pest in various management conditions. COSMOS can be seen as a 'virtual laboratory' (Charnell, 2008) for studying different agricultural practices that can influence the epidemiology of a pest. Emergence of population spatial properties from individual biology is the main driver of our study, as we consider that these practices will influence the individual behaviour of pests. In that way, IBMs can be applied to several pests, for which the spatial heterogeneity of agricultural practices influences biological parameters of individuals.

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Appendix A

Twenty biological parameters of the insect (k “factors”, according to the Morris method) were tested, considering their possible influence on the variability of mean and standard deviation of attacks. Each tested range was divided into 4 levels, corresponding to the resolution (Δ) at which the factor was examined. Following the method, for each factor, one of the four possible levels was randomly chosen, leading to a first sample. A first sensitivity run was done on this sample that consisted of 100 replicates of a one cropping-cycle (200 time steps) simulation (see § 3.2); the results were further averaged over the 100 replicates. Starting from the first factor sample, similar sensitivity runs were performed by considering successively each factor and increasing (or decreasing) its value by the quantity Δ . The combination of these $(k+1)$ sensitivity runs is called a trajectory and has to be repeated r times, thus leading to $r(k+1)$ sensitivity runs.

The elementary effect (EE_i) of a parameter θ on a trajectory j was calculated as:

$$EE_{i,j}(\theta) = \frac{y_j(\theta + e_i\Delta) - y_j(\theta)}{\Delta} \quad (\text{A.1})$$

with $e_i = \pm 1$ and y_j the model output, here the mean or variance of attacks in the plot.

Thus, we generated a design experiment of 20 levels of parameters on 30 trajectories, which corresponded to a series of 630 sensitivity runs. The mean μ and the standard deviation σ of the absolute values of the elementary effects over the trajectories were used as sensitivity measures to ascertain the importance of the factors. A large μ indicates a large overall influence of the parameter and a large σ implies a dependency of the parameter on the value of the other parameters through non-linear or interaction effects.

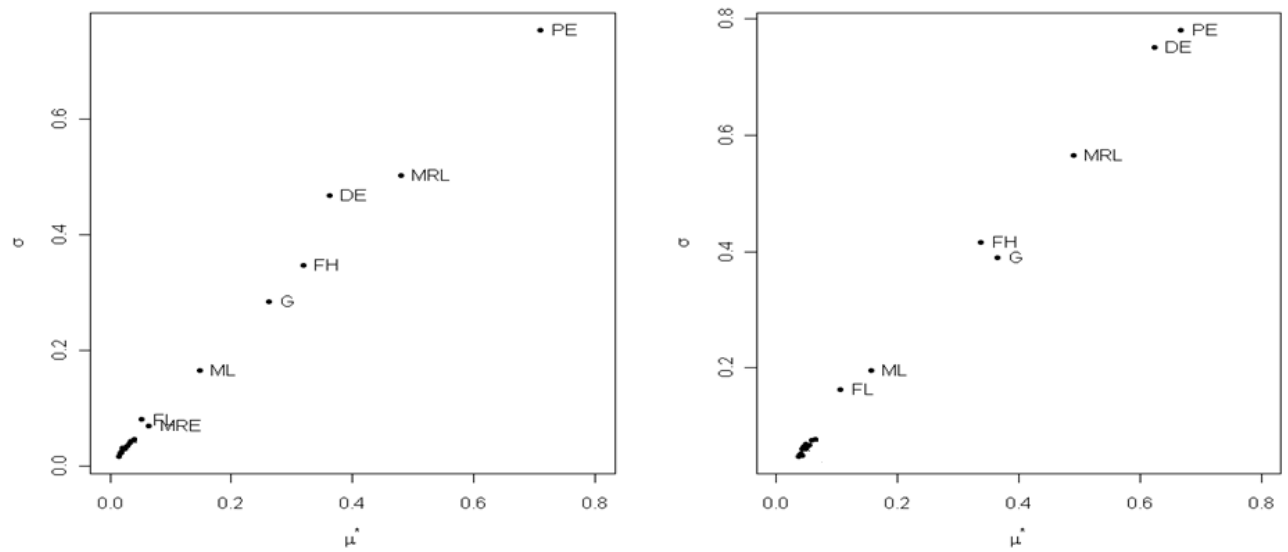


Fig. A.1- Sensitivity analysis on mean (x axis) and standard deviation (y axis) of attacks of *C. sordidus*. For each parameter, the tested range was defined according to the uncertainty of estimates according to published experimental studies.

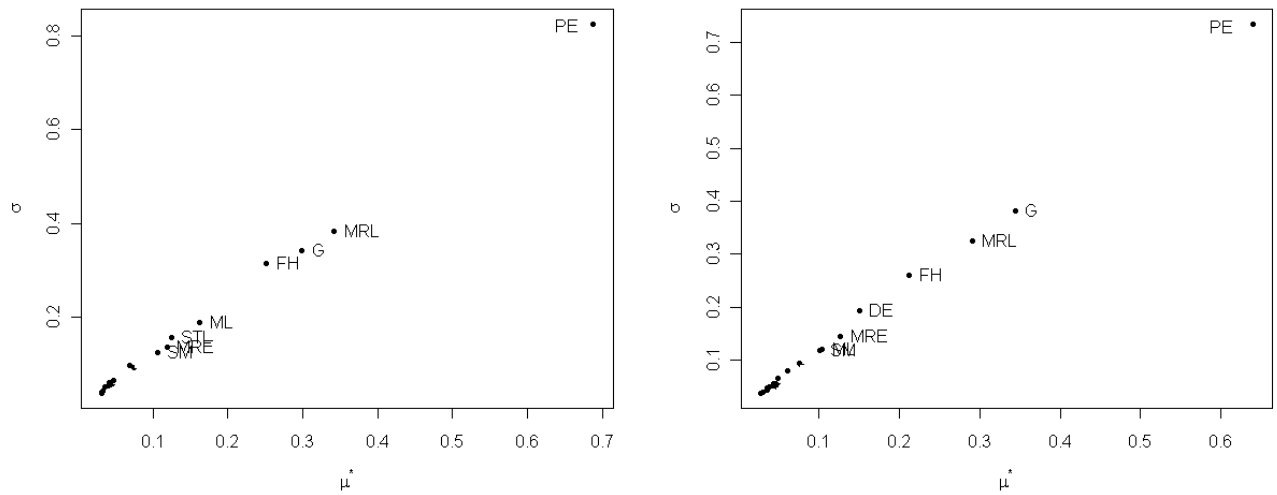


Fig. A.2- Sensitivity analysis on mean and standard deviation of attacks of *C. sordidus*. For each parameter, the tested range was equally proportioned (-20%, -10%, 10%, 20% of the value in Table 1).

CHAPITRE VI – APPLICATION DU MODELE COSMOS A CONCEVOIR DES ARRANGEMENTS SPATIAUX DE PIEGES ET DE PLANTATIONS

La protection intégrée d'une culture contre un ravageur allie trois composantes: agronomie, écologie et socio-économie. Elle nécessite une vision globale du système et de tous ces acteurs, du ravageur à l'agriculteur. La modélisation mécaniste apporte une vision synthétique des processus du système. Elle répond à l'objectif principal de limiter la population d'un ravageur, en jouant sur les processus écologiques du système. Ce chapitre propose une exploration des propriétés émergentes du modèle COSMOS tel que paramétré et évalué dans les Chapitres IV et V. Ce chapitre redéveloppe la méthode de calcul des potentiels de préférence et des fonctions de portée exposés dans le Chapitre IV, en associant le piège aux habitats estimés. Les données nécessaires à l'estimation du potentiel du piège ont été récoltées selon la technique de télémétrie exposée dans le Chapitre III. Les essais correspondant à l'estimation des potentiels des éléments d'habitat sont l'ensemble des essais figurant en **Annexe A** de fin de thèse. D'autre part, le travail de simulation de cette partie est réalisé à une échelle spatiale plus large que dans les Chapitres IV et V d'où un rallongement des temps de calcul et la recherche d'une interface de programmation plus rapide, en l'occurrence Netlogo (**Annexe C**).

Ce chapitre repose sur l'article à soumettre à *Agriculture, Ecosystems & Environment* et intitulé: **From IBM to IPM: How to use individual-based models to design spatial arrangement of traps and crops**. Son objectif appliqué est d'analyser comment (i) la disposition spatiale des pièges lorsque les parcelles sont placées en jachère, et (ii) la fragmentation de la zone plantée affecte les densités de charançons au champ. Le manuscrit propose un cadre de travail pour modéliser des arrangements spatiaux d'habitats à différentes échelles spatiales afin de sélectionner l'arrangement spatial limitant la population du ravageur étudié. Il s'agit également, à partir d'un cas d'étude, d'analyser l'utilité des IBMs pour aider à la définition de stratégies de gestion des bioagresseurs.

From IBM to IPM: How to use individual-based models to design spatial arrangement of traps and crops

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1. Introduction

In the past, pesticides were considered as the main solution to control populations of insect pests (Lewis et al. 1997). Today, researches on pest control point toward a more comprehensive and global vision of interactions between insects and plants, through a better understanding of related ecological processes. Foraging behaviour studies have promoted the "push-pull" strategy based on the use of repulsive and attractive crops, or pest control measures based on the destruction of resource by fallow. Studies of communication between individuals have been useful for mass trapping or mating disruption (Khan et al. 2008).

Among the global methods of pest control, Integrated Pest Management (IPM) combines biological and other controls in complementary ways to maintain pest population within acceptable bounds (Lewis et al. 1997). IPM sits on several pillars, including chemical ecology (Khan et al. 2008), behavioural ecology (Roitberg 2007), and cultural practices (Castellazzi et al. 2007). Its main objective is to integrate the use of these pillars in a complementary way. IPM is at the interface between three universes: ecological, socioeconomic and agricultural (Kogan 1998). Thus, it is important to consider the feasibility of IPM measures, not only from a technical point of view (e.g. the density and arrangement of plants), which may participate to IPM, depends on the crop species, the quality of soil and the type of agricultural machine, but also from a socioeconomic point of view: in the developing countries, the use of high-cost cultural techniques is impossible.

Space is now considered as a key element for IPM that should consider the management of field margins (Musters et al. 2009), the effects of habitat fragmentation and connectivity (Diekotter et al. 2008; Valladares et al. 2006), spatial organisation of fallows (Rhino et al. 2010), and trap spacing (Bacca et al. 2006). Furthermore, habitat features change across scales, as plant distribution will be more homogeneous at field scale than landscape scale, spatial heterogeneity of landscape being closely linked to agricultural intensification (Benton et al. 2003). So, population distribution of pests is not equally influenced by habitat features at all spatial scales (Gaucherel et al. 2007) and we need to consider the effect of scale on management practices.

For insect pests, the environment can be considered as a series of patches of different suitability level, shape, size and isolation level in an unsuitable matrix (Tscharntke et al. 2002). The spatial heterogeneity of the landscape matrix will greatly influence movements, egg-laying tactics and mortality risks of insects and consequently their spatial distribution and related damages (Huffaker and Gutierrez 1999). It is especially important to understand how environmental heterogeneity affects the movement in order to use it as a lever in an IPM context. The movement can be considered as a dynamic process affected by behavioural (foraging, resting, etc.) and external components (composition of the environment). Radiotracking techniques associated with circular statistics or discrete choice models help measuring the dynamic component of insect movement (Vinatier et al. 2010a). It is possible to disentangle the movement in a dynamic process to be included in a mechanistic model, as shown by Rhodes et al. (Rhodes et al. 2005). Mechanistic models, by simulating explicitly ecological processes, can help exploring the effect of spatial heterogeneity controlled by cropping practices (Potting et al. 2005; Tyutyunov et al. 2008a; Tyutyunov et al. 2008b). Models are chosen according to their capacities to account for the spatial arrangement of habitat features and interactions among individuals (Vinatier et al. 2010b). Among

mechanistic models, individual-based models (IBMs) are well suited for studying the relationship between populations and their environment, following the principle of emergence of population properties from individual behaviours (Grimm and Railsback 2005). In IBMs, each individual is explicitly modelled and acts according to a set of rules depending on the landscape structure that is represented on a grid. IBMs are spatially explicit as exact locations of each habitat element and each individual are known. The heterogeneity of the landscape matrix can be virtually modified and, therefore, it can be considered as a variable in IPM studies.

This paper presents a framework to design the spatial organisation of traps and crops through the use of IBMs. It describes (i) how to link radiotracking data to a spatially explicit model and (ii) the analysis of spatial patterns with respect to insect limitation. We took as case study the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae), living in a heterogeneous agroecosystem of bananas. We attempted to answer the question: What is the effect of trap arrangement in a fallow and fragmentation of banana patches on the level of populations?

2. Materials and methods

2.1. Study species and study site

Cosmopolites sordidus is a walking insect with a nocturnal and cryptic activity living in all countries where its unique host-plant, the banana, is present (Gold et al. 2001). Adults prefer moist environments and feed on banana plants and residues. Females lay eggs at the base of the host-plant, and the larva grows inside the corm of the plant.

They live in agroecosystems where field is considered as a mosaic of different elements having a potential effect on dispersal abilities of adults. The matrix of the field is principally

composed of mats of banana plants, crop residues, bare soil and ditches. Banana plants are considered to be semiperennial, and plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner 1994). Only one sucker per mat is selected by farmers. Banana leaves, trunks of harvested plants, and rejected suckers are regularly cut by farmers all the year to supply cover of crop residues.

The duration of banana plantations depends on production areas. In intensive areas, like French West Indies, Costa Rica, or Brazil, they last approximately five years, i.e. six successive cropping cycles before destruction. In more extensive agricultural areas, such as Africa, banana production lasts much longer, sometimes without any destruction. At the end of a banana production, plants are killed by the injection of herbicides. After destruction, the field is left lying fallow during approximately one year.

The control of *C. sordidus* populations is based on pheromone mass trapping (Rhino et al. 2010). Yellow pitfall traps containing an aggregation pheromone are buried in the soil. The pheromone used in the traps is based on the aggregation pheromone called sordidine, which is emitted by *C. sordidus* males (Beauhaire et al. 1995).

Despite the recent advances in the control of *C. sordidus* by the combination of fallow and mass trapping (Rhino et al. 2010), there is a need for further investigations on the selection of the best spatial arrangement of traps.

2.2. The spatial explicit model of population dynamics

Simulations are based on a modified form of the individual-based model developed earlier on this pest (Vinatier et al. 2009). The model runs on a daily time step. The processes underlying the spatial pattern of the insect are explicitly modelled at individual level. The environment is spatially explicit and represented by a grid of cells containing habitat elements that are mutually exclusive (banana plant, crop residues, trap, ditch or bare soil) and/or agents

(insects, banana plants). The grid is considered as toroidal to avoid edge effects in the simulations. Each agent passes through different stages: egg, larva, pupa, adult for insects and maiden sucker, preflowering, post-flowering, and harvesting stages for banana plants. Insects act according to a set of rules depending on the properties of their current location. Egg-laying of females, which occurs only on cells with banana plants, depends on the density of adults on the cell and on the stage of the banana plant. The development of plants, eggs, larvae and pupae are temperature-dependent. The mortality of each insect stage is considered as constant in the model. The infestation of each banana plant is measured as the total number of larvae that have reached emergence multiplied by mean diameter of a gallery.

We considered a range of habitat elements to modify the dispersion process of the previous model, which was determinist and only from plant to plant. Each cell was represented by a habitat element (T, trap; P, host-plant; C, crop residues; B, bare soil; and D, ditch) and the movement was discrete from one cell to another. A maximal cell size of 1 meter was chosen to characterize the habitat variability, following Marzluff et al. (2004). The probability of moving from a cell a to a cell b in the grid within a temporal unit was a first-order Markov chain defined as:

$$\Pr(a \rightarrow b) = \frac{\alpha_{h(b)} f_{\beta_h}(d_{ab})}{\sum_{k=1}^m \alpha_{h(k)} f_{\beta_h}(d_{ak})} \quad \text{Eq. 1}$$

where $\alpha_{h(k)}$ is the relative preference for habitat h of cell k , d_{ak} the distance between cells a and k and $f(d_{ak})$ the dispersal kernel depending on this distance of the form $\exp(-\beta_a d_{ab})$. The individual decision to move was based on a multinomial probit between all the probabilities calculated over the grid. For calculation efficiency, the cells with probabilities about zero were not considered in the multinomial probit.

2.3. Estimation of the dispersal parameters

The ten unknown parameters (α_h and β_h with $h=[T, P, C, B, D]$) were estimated via maximum likelihood estimation (Nelder and Mead 1965) on the basis of a radio-tracking dataset measured on this species (Vinatier et al. 2010a). Constraints were added in the model: the sum of alphas equals one and each parameter is positive. β_T was fixed to 100 to account for the fact that the probability of escaping the trap is null.

The radio-tracking data set consisted of pairs of daily observations of approximately 800 males and 800 females of *C. sordidus* followed in seven different plots, in which the mosaic of habitats was experimentally manipulated (for more details on the tracking method, see Vinatier et al. 2010a). Locations of insects and habitat elements were noted on a one-meter cell grid that corresponded to the resolution of the model.

2.4. Optimal spacing of traps in an intensive banana plantation in fallow

In areas of intensive production, banana plantation lasts almost six years, and then it is destroyed by an herbicide application to be in fallow (Lassoudière 2007). Fallow area corresponds to one ninth of the total area.

The virtual banana field on which heterogeneity was manipulated was a 96x96 cells grid, with a fallow area in a central square ring of 32x32 cells. This corresponds to a common situation in banana cropping systems, when the field lied in fallow is surrounded by other planted fields (Lassoudière 2007). As in real situations, banana plants were regularly planted (2 m x 2 m) at a density of 2200 bananas/ha.

We tested a permanent arrangement of mass trapping during one year in the field described before. It was necessary to choose a trap density that did not exceed 16 traps/ha, as a higher density would be too costly for long-term monitoring. 16 traps were disposed along a

square ring centred to the centre of the plot, or on a regular network over the grid (**Figure VI-1**). In the first case, we varied the diameter of the ring from 1 to 30 meters. In all cases, adults of *C. sordidus* were randomly set all over the grid at a density of 1500 individuals/ha. Simulations were repeated 20 times over one year. The density of adults and the number of adults captured per trap were recorded one month and one year after the beginning of the simulations.

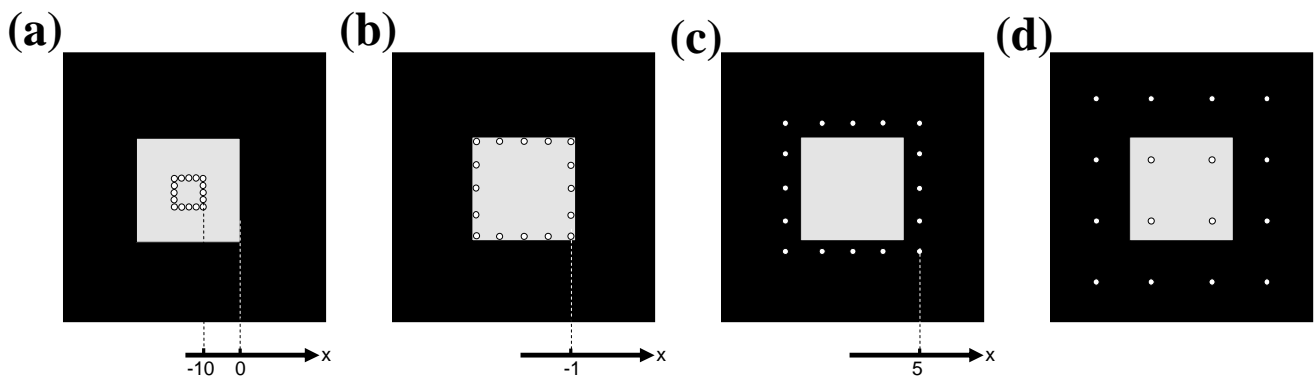


Figure VI-1. Examples of spatial trap arrangements in a square ring at (a) -10 metres, (b) -1 metres, and (c) 5 metres from the border of the field, according to direction of x-axis; and (d) regularly distributed over the grid. The trap location is figured by a white point. Banana and fallow areas are in black and light grey, respectively.

2.5. Fragmentation and size effects in extensive banana plantations

In areas of extensive production, bananas are regularly planted (2m x 2m) in patches of varying sizes (Lassoudière 2007). We considered a grid consisting of banana plants and bare soil in the proportion 1:9. At initialisation, grid was composed of 2200 bananas/ha and 1500 weevils/ha. We tested the effect of varying patch fragmentation through six spatial patterns (from $4^0=1$ patch to $4^5=1024$ patches) for three different sizes of field (48x48, 96x96 and 192x192 cells). We tested also the effect of 5 different sizes of a field with the same pattern (one patch of regularly planted banana at the same density in the middle of the field, corresponding to a one-patch pattern).

2.6. Statistical and modelling tools

The platform used to develop the model was the Netlogo software (Wilensky 1999). All statistical analyses were performed with the R software (R Development Core Team 2009) using basic and applied packages: "lattice" (for plotting level plots), "spatstat" (for spatial analyses) and "stats4" (for maximum likelihood estimation).

3. Results

3.1. Estimation of the dispersal parameters

Table VI-1 shows that trap was the most preferred habitat. Then host plant and crop residues were equally preferred, whereas bare soil and ditch were much less preferred (**Table VI-1**). Regarding parameter β , which defines the shape of the dispersal kernel, the higher the value of β_i for the current habitat i , the more the individual stayed in habitat i . The value of β_i was highest for the host plant or the crop residues, intermediate for the bare soil, and lowest for the ditch (**Table VI-1**). Consequently, the movement rate was highest when the current habitat was ditch, was intermediate for bare soil, and was the lowest for crop residues and host plant.

Table VI-1. Parameter estimates of the movement process of *C.sordidus* in the individual-based model, from the radio-tracking dataset.

Mean			Standard error		
Relative habitat preference			Parameter of the dispersal kernel		
α_T	0.86357375	0.0227554224	β_T	100	fixed
α_P	0.07559439	0.0129049226	β_P	2.06518544	0.0368306669
α_C	0.05181051	0.0089547495	β_C	2.09589287	0.0479089734
α_B	0.0064581	fixed	β_B	1.09817321	0.0253469307
α_D	0.00256325	0.0004704881	β_D	0.72382497	0.1040634209

Note: The letters indicate the habitat type: T, trap; P, host plant; C, covered soil; B, bare soil; D, ditch.

3.2 Optimal spacing of traps in a fallow surrounded by a banana plantation

Figure VI-2 shows the influence of the spatial arrangement of traps on insect limitation and trap efficiency. For traps disposed in a square ring, after one month of simulation, there was a peak of trap efficiency when traps were disposed at the fallow-banana interface (**Figure VI-2a**). The peak was due to the concentration at this interface of weevils that escaped the field in fallow, as proven by density of weevils' residence time in each cell (data not shown). This concentration was not visible after one year of simulation, as insects were absent from the field in fallow. After one year of simulation, the trap efficiency was maximal in the banana area and plateaued at more than ten meters from the fallow-banana interface. Both short and long term effects indicated that the traps located in the banana area were more efficient than those located in the fallow area. In the fallow area, the weak efficiency of traps that were distant from the fallow-banana interface was supposed to be due to the grouping of traps, which increased the competition between traps. **Figure VI-2b** indicates a direct effect of trap efficiency on the density of weevils per ha, particularly pronounced after one year of simulation. In that case, the density of weevils was the lowest and the highest for a trap ring located between 5 and 15 meters from the interface in the banana and fallow areas, respectively. Long-term results indicate that the number of catches, and, consequently the resulting density of weevils per ha were similar for traps regularly spaced and for traps disposed in a square ring at the banana-fallow interface.

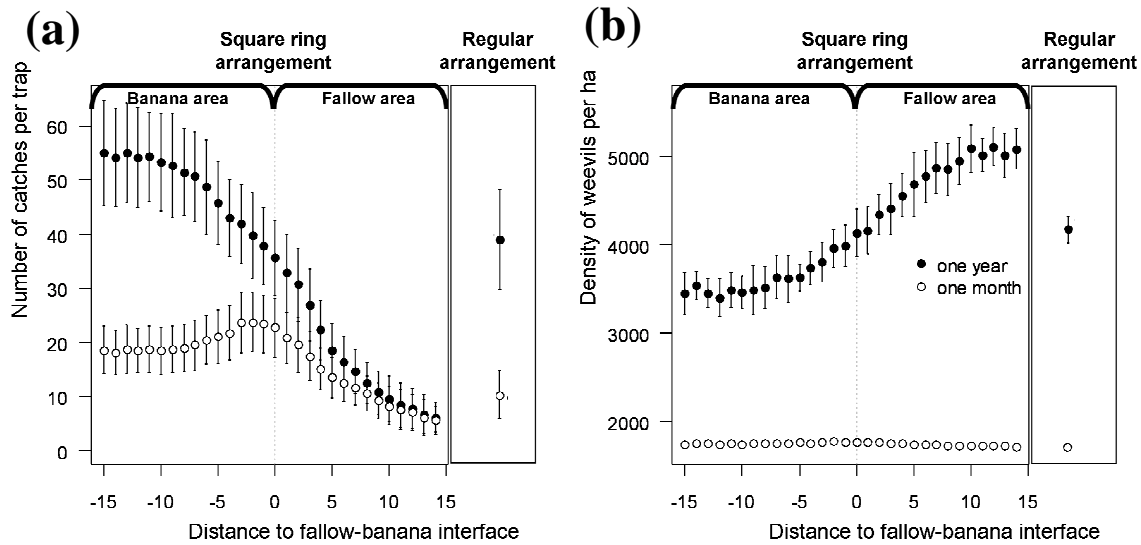


Figure VI-2. Means (points) and standard deviations (bars) of trap efficiency (a) and density of weevils per ha (b) against distance to fallow-banana interface after one-month and one-year simulation using the COSMOS model. Standard deviations are issued from 20 runs of the model.

3.3. Fragmentation and size effects in extensive banana plantations

Figure VI-4 shows the effect of fragmentation on weevils' density after one-year simulations. The weevils' density increased with fragmentation level and reached a plateau with a number of patches exceeding 4, 16, and 64, for a field of 48x48 cells, 96x96 cells and 192x192 cells, respectively.

Figure VI-5 shows the effect of varying size of a field with the same pattern (one patch-pattern). We observed a decrease of the weevils' density when the size of the field increased. Variability of the results issued from 100 runs of the model decreased with the size of the field. We found similar results when we took the four-patch pattern (data not shown).

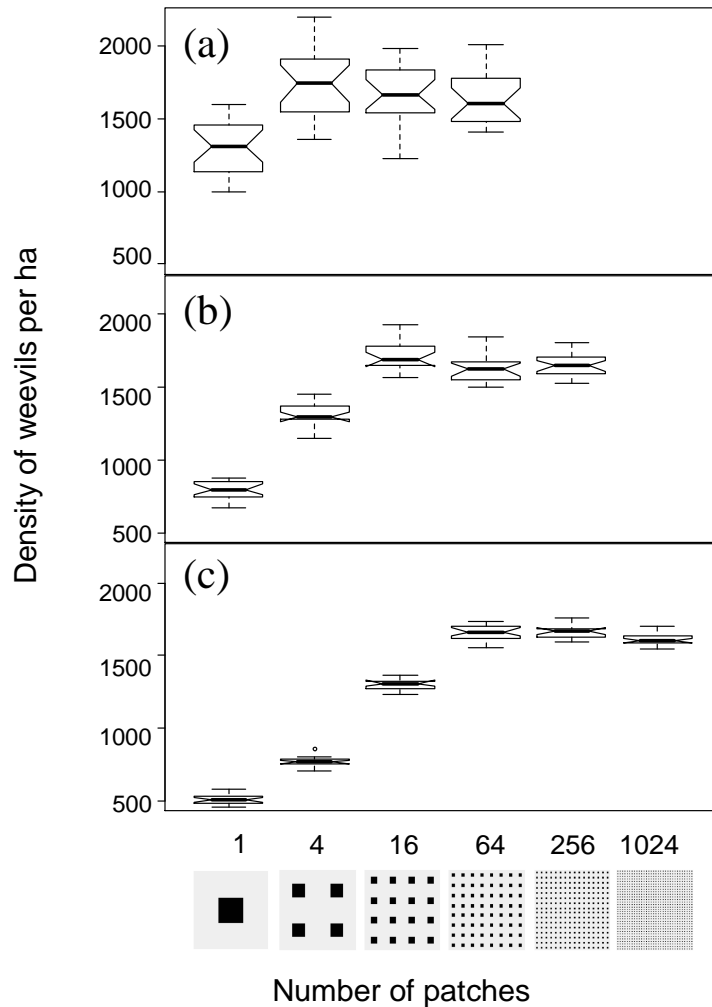


Figure VI-3. Boxplot of the density of weevils per hectare after one-year simulation using COSMOS model for 3 sizes of fields (a) 48x48 cells, (b) 96x96 cells, and (c) 192x192 cells through different level of plant fragmentation. At initialization, weevils were randomly distributed on the fields. Each boxplot is issued from 20 runs of the model. Each cell is one meter length.

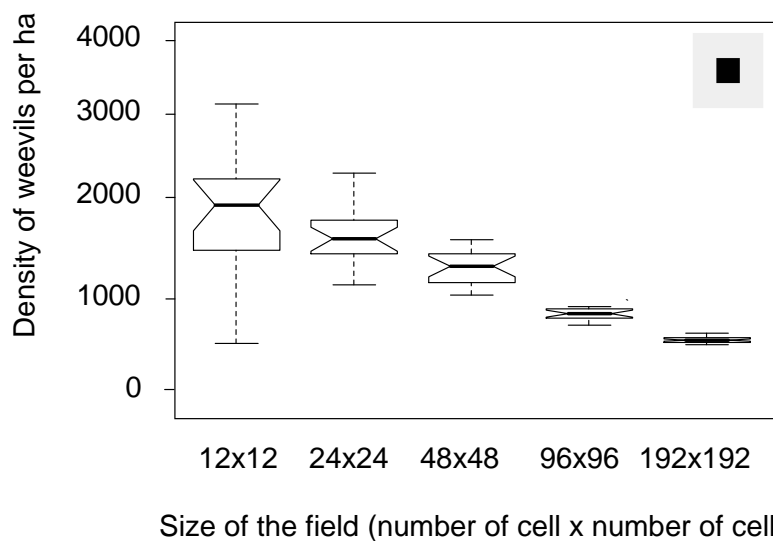


Figure VI-4. Boxplot of weevils' density per ha for different size of fields with the same pattern (one patch of regularly planted banana at the same density in the middle of the field, figured on the top-right of the figure) after one-year simulation using the COSMOS model. At initialization, weevils were randomly distributed on the fields. Each boxplot is issued from 20 runs of the model. Each cell is one meter length.

4. Discussion

According to the decomposition of movement in a discrete choice model, attractiveness of habitats was ranked in the following ascending order: ditch, bare soil, crop residues, banana plant and trap. Dispersal range of habitats followed the inverse ranking of attractiveness, i.e. the ditch was the less attractive element with the highest dispersal range. Trap was the most attractive element in banana plantations, confirming its interest in mass trapping (Gold et al. 2001). The attractiveness of traps was 11 and 133 times higher than that of banana plants and bare soil, respectively. It appears also that the efficiency of mass trapping would be better when traps are disposed in fallows, in accordance with the results found by Rhino et al. (2010).

The mass trapping method applied in this study aims at containing the insect population below reasonable bounds. The results of the simulation procedure indicate that the banana-fallow interface is a crucial area to arrange the traps when looking for short term effects. In our study, we explained population level in transition zone by population movement, which was higher in unsuitable areas than in suitable areas. Longer effects indicate a progressive increase of trap efficiency for those located in banana area, as weevils have escaped the fallow area. This transition zone has also an important consequences in terms of species richness, as indicated by Tschardt & Brandl (2004). They demonstrated that species richness is higher in the transition zone between a patch and some adjacent habitat type because of environmental or human conditions.

The second simulation procedure addresses the questions of patch fragmentation. Patch fragmentation increased with the density of weevil's population. Indeed, a highly fragmented area of bananas allows a largest cover of the grid with connected patches of banana plants. In such a situation, the randomly distributed population of weevils is more able to reach a suitable patch than in a spatial pattern consisting of one unique central patch of

plants, especially for insects located far away from the patch. At field scale, this result contrasts with Haynes et al. (2007a) that found experimentally no effect of micro-fragmentation on density of flying insects (*Melanoplus femurrubrum*). At landscape scale, Pichancourt et al. (2006) found with a modelling approach that a single large patch of wood is better than several small patches with respect to the level of a crawling insect (*Abax parallelepipedus*) population. They argued that highly fragmented landscapes allow insects to die more frequently when they move between patches. In our case, mortality factors are not dependent on habitat moved through, so that the main source of population loss is due to individuals that fail to find a suitable patch. Increasing size of the field with the same pattern limits population of weevils. Perceptual range of the banana weevil is moderate and it is not able to assess the pattern in large fields.

This result has important consequences in terms of management practices, as areas of planted bananas may vary widely between farmers in developing countries, and a field planted according to a given pattern at a given size will not give the same results at a larger size. The results point toward a limitation of banana area fragmentation to limit populations of weevils.

5. References

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CHAPITRE VII – DISCUSSION GENERALE

1. Les apports du travail

L'objectif principal du travail était de comprendre et de modéliser les processus structurant la dynamique spatiale des populations de charançons et leur épidémiologie. Il était donc nécessaire d'analyser, de quantifier et de décomposer le mouvement du charançon afin de l'intégrer dans un modèle mécaniste de déplacement. Ensuite et afin de travailler à une échelle temporelle plus large, des processus démographiques tels que mortalité, fécondité et développement des immatures ont été ajoutés au modèle pour simuler des attaques de parcelles sur une ou plusieurs années. *In fine*, le modèle ainsi construit doit permettre d'aider à la définition d'aménagements parcellaires permettant la diminution des populations de charançons, en jouant sur l'interaction entre les processus du modèle et l'hétérogénéité de l'habitat.

1.1. Les relations entre insecte et environnement

L'étude de télémétrie a permis de caractériser le mouvement du charançon adulte, puis de sélectionner les facteurs qui l'influencent. Le mouvement du charançon est limité, peu corrélé, de type subdiffusif, avec une forte variabilité individuelle. Parmi les facteurs explicatifs du mouvement, les statistiques circulaires appliquées aux données de télémétrie ont révélé une forte influence des éléments du paysage sur le déplacement des individus. Les trajectoires des charançons sont orientées selon les lignes de plantation des bananiers et les bandes de résidus de culture. Par contre, le sexe et le climat n'influencent pas les statistiques de mouvement. La méthode de suivi par télémétrie exposée dans le Chapitre III n'avait encore jamais été appliquée à un insecte marcheur de cette taille dans les conditions au champ. Les rares essais sur insectes portaient sur des individus sociaux (Molet et al. 2008; Robinson et al. 2009; Streit et al. 2003) pour étudier des patterns d'activité et non des capacités de déplacement.

Sachant l'importance du contexte spatial dans le mouvement du charançon, il s'agissait de tester l'hypothèse d'une perception de l'espace dépendant de l'habitat de résidence de l'individu. Dans notre approche, chaque déplacement est considéré comme discret et dépend des caractéristiques de l'habitat de départ et de destination. La perception de l'espace dépendante de la cellule de départ et le potentiel de préférence d'une cellule de destination ont été estimés pour chaque type d'habitat par maximum de vraisemblance. Ce processus markovien, une fois identifié et estimé, a été incorporé dans un modèle mécaniste, stochastique et individu-centré. Le modèle a permis de valider l'intérêt d'une perception de l'espace dépendante de l'habitat de départ, en comparant les patterns d'utilisation de l'espace simulés par le modèle aux patterns réels. **Dans notre cas d'étude et d'après le Chapitre VI,**

le piège est l'élément le plus attractif pour le charançon, suivi par les bananiers et les résidus de culture, tous deux ayant une attractivité comparable. Ravine et sol nu sont les éléments les moins attractifs pour le charançon. Les étendues des perceptions d'espace suivent l'ordre inverse des préférences d'habitat : l'habitat le moins attractif est celui où la perception de l'espace est la plus étendue. **A un niveau plus général**, l'étude du mouvement telle qu'exposée dans le Chapitre IV a montré l'importance de l'habitat de départ dans la perception de l'espace d'un individu, hypothèse n'ayant été que suggérée par Rhodes et al. (2005). D'autre part, la fonction de déplacement intégrée dans le modèle mécaniste est très différente de la plupart des modèles individu-centrés. En effet, dans notre cas, le choix d'une cellule se fait selon une loi multinomiale dépendant de l'ensemble des potentiels des cellules, alors que dans la plupart des autres modèles individu-centrés, le déplacement se fait de manière déterministe vers la cellule ("best cell") ayant le plus fort potentiel (Grimm and Railsback 2005). Cette nouvelle approche apporte plus de réalisme au mouvement, où l'individu passe parfois par des habitats moins attractifs. Ce formalisme semble adapté à des organismes qui ont une capacité de dispersion modérée ou dont la perception est altérée par l'environnement proche. Dans le cas des ravageurs des cultures, un formalisme "habitat-dépendant" permettrait de tester l'effet barrière ou corridor de certains éléments d'habitat, afin de modifier la dynamique spatiale des populations.

1.2. Le lien entre processus démographiques et infestation

Afin de comprendre les processus expliquant les niveaux d'attaques des charançons dans les parcelles, l'ensemble des traits de vie de l'insecte a été intégré au modèle mécaniste développé ci-dessus. Les traits de vie à intégrer au modèle ont été choisis et calibrés en fonction des données bibliographiques disponibles et du processus à expliquer. Le processus de ponte des femelles est dépendant des densités d'adultes présentes et du stade de développement du bananier, ce dernier étant température-dépendant. Le taux de mortalité journalier des adultes est considéré en première approximation comme constant de l'émergence des adultes à la longévité maximale observée en laboratoire. Le développement des stades préimaginaux est dépendant de la température. Le modèle, considéré ici comme *ad hoc*, relie avec succès les processus d'intérêt (cachés) aux observations dont on dispose, à savoir les statistiques d'attaques de micro-parcelles de bananiers. **Dans notre cas d'étude**, l'analyse de sensibilité des paramètres du modèle a révélé l'importance du taux de prédation des œufs par les ravageurs, des paramètres démographiques des adultes et des taux de mortalité larvaires dans la compréhension des statistiques d'infestation. **A un niveau plus général**, l'approche modélisatrice développée dans le Chapitre V est intéressante pour deux raisons: d'une part, il s'agit d'un modèle qui a été confronté directement aux données de terrain, procédure peu appliquée dans le domaine de la modélisation individu-centrée. D'autre part, la méthode d'analyse de sensibilité de Morris (Morris 1991) n'avait jamais été conduite sur des modèles mécanistes. Les analyses de sensibilité généralement réalisées sont de type OAT ("one

parameter at a time") et ne permettent pas de distinguer des effets non linéaires, à l'inverse de la méthode de Morris (Saltelli et al. 2000). Cette analyse a permis de hiérarchiser *a posteriori* les processus prépondérants par rapport à l'objectif de l'étude, qui est de simuler la dynamique populationnelle du charançon sur le long terme. **D'une manière générale, cette thèse a tenté de relier plusieurs facettes d'une approche scientifique qui sont souvent disjointes en écologie: les statistiques (spatiales ou non), la modélisation mécaniste et l'expérimentation au champ.**

1.3. Applications du modèle au système de culture bananier

Le modèle COSMOS a permis de tester les propriétés populationnelles émergeant des relations entre l'hétérogénéité de l'environnement et la dynamique spatiale des individus. D'une part, le modèle indique que le temps de colonisation des parcelles dont les bananiers sont plantés en paquets est plus long mais le pourcentage de pieds sévèrement attaqués est plus élevé que lorsqu'elles sont plantées régulièrement ou en double rang. D'autre part, le niveau moyen d'attaque est beaucoup plus élevé dans les bananeraies désynchronisées plutôt que synchronisées. Dans le cadre d'une mise en jachère, la disposition des pièges dans la zone d'interface entre la zone plantée et la zone de jachère offre la meilleure efficacité à court terme. Après un an de jachère, il s'avère que les pièges placés dans la zone de bananeraie permettent de diminuer significativement les densités de charançons, contrairement à ceux placés dans les zones de jachère. A l'échelle d'une grande parcelle, la fragmentation de la zone de bananeraie augmente les densités de charançons au champ. Ce sont principalement les propriétés exploratoires du modèle qui sont mises en avant dans notre dernière étude, dans des conditions de simulations pour lesquelles la confrontation aux données réelles était impossible par manque de données disponibles.

1.4. Conclusion sur les apports méthodologiques

Cette thèse exploite des outils novateurs dans le domaine de l'écologie spatiale (approche de suivi par télémétrie, combinaison des statistiques et des modèles). L'approche de télémétrie exposée dans la thèse offre des applications variées dans le domaine du suivi du mouvement des insectes marcheurs. Globalement, la décomposition du mouvement que nous avons proposée offre de nouvelles perspectives dans la compréhension des déplacements d'organismes fortement conditionnés par l'hétérogénéité de l'habitat, elle est également générique et peut s'appliquer à d'autres modèles biologiques de déplacement. Il serait possible d'appliquer la loi de décomposition à certaines espèces de coléoptères suivies par radiotélémétrie dans un but de conservation des populations, cette fois (Ranius 2006). La thèse montre l'intérêt de combiner les statistiques spatiales et les modèles mécanistes dans une seule et même démarche de compréhension d'un processus. Cette dernière approche est mise en évidence par l'étude bibliographique du Chapitre II et illustrée dans le Chapitre IV. Le

modèle permet de sélectionner les configurations spatiales de pièges et de parcelles intéressantes dans la lutte contre le charançon. Il apparaît nécessaire par la suite de tester ces configurations dans le cadre d'une expérimentation au champ. En même temps qu'il permet d'étudier l'impact des facteurs « exogènes » que sont ces configurations, le modèle permet d'étudier par simulation la réponse d'indices spatiaux de population, résultant de dynamiques spatio-temporelles, à la modulation de facteurs « endogènes » comme la mortalité des juvéniles, la dispersion, ou la fécondité des adultes. Le modèle est ainsi un outil intéressant pour répondre à un objectif crucial en écologie spatiale, qui est de comprendre comment les processus démographiques et le mouvement affectent la distribution spatiale des populations.

2. Retour sur les choix méthodologiques

2.1. Limites et domaine de validité des approches

La décomposition du mouvement a nécessité certaines approximations en négligeant les effets du sexe et du climat sur les statistiques des trajectoires (Chapitre III). Néanmoins, ces facteurs peuvent affecter le mouvement à une échelle temporelle plus longue que celle de l'expérimentation. Par exemple, les expérimentations ayant eu lieu en saison sèche, il serait intéressant de réaliser les expérimentations en saison humide. D'autre part, certains facteurs, comme l'âge et le poids des individus peuvent influencer le mouvement et n'ont pas été sélectionnés. Dans le modèle de décomposition choisi, on a négligé la corrélation entre mouvements élémentaires qui a été mise en évidence dans le Chapitre III, même si cette dernière est très faible. En considérant comme linéaires les segments de trajectoires entre deux relevés séparés par une nuit, on néglige les mouvements intermédiaires entre ces deux relevés. Il aurait fallu suivre quelques charançons pendant une nuit en réalisant des relevés toutes les dizaines de minutes pour évaluer le biais induit par la non-considération des mouvements intermédiaires.

La construction du modèle COSMOS a nécessité de sélectionner a priori les processus permettant de répondre à l'objectif principal du travail qui est de manipuler l'habitat pour limiter la population d'un insecte. Une fois la question de recherche posée, il a fallu identifier les principaux processus en jeu, et la résolution spatiale ($\text{m}^2/\text{hectare}$) et temporelle (jour/année) adéquate pour rendre compte de ces processus. Parmi les processus sélectionnés dans le modèle, le mouvement en fonction des éléments du paysage et les processus démographiques d'interaction avec la plante-hôte (densité-dépendance des pontes, fécondité dépendante du stade de la plante-hôte) ont été privilégiés car ils sont directement influencés par l'organisation spatiale du parcellaire, considérée comme manipulable par les planteurs.

Or il existe des processus dépendant de facteurs "non manipulables" ou non influencés par l'organisation spatiale de l'habitat qui n'ont pas été pris en compte dans le modèle. Par exemple, l'âge-dépendance de la fonction de reproduction (Delattre 1980), l'influence du

climat (vent, humidité) sur l'efficacité des pièges (Rhino et al. 2010), les interactions locales entre individus (aggrégation, densité-dépendance du mouvement) (Cuillé 1950). Les deux premiers facteurs n'ont pas été sélectionnés car leur existence est contestée suivant les auteurs (Gold et al. 2001; Tinzaara et al. 2005b). Les densités de charançons suivies par télémétrie et la précision de la méthode n'ont pas permis de quantifier le dernier facteur. Dans le dernier cas, je suppose que ces processus agissent à une échelle spatiale inférieure à celle de mon modèle.

Dans le Chapitre V, le modèle a été construit selon un unique jeu de processus. Ce jeu de processus définit l'unique hypothèse de travail du modèle. Accepter cette hypothèse de travail au regard d'une confrontation validée aux données réelles ne permet pas de rejeter des hypothèses ou jeux de processus alternatifs (McIntire and Fajardo 2009). Or plusieurs jeux de processus peuvent conduire au même résultat lors de la phase de validation du modèle. Il est donc préférable de confronter plusieurs hypothèses de travail aux données réelles afin de sélectionner les plus pertinentes (Grimm et al. 2005).

2.2. Pourquoi avoir choisi un modèle individu-centré et spatialement explicite?

Il apparaît nécessaire de revenir sur les raisons du choix de modélisation *a priori*, au regard des nouveaux éléments fournis par la thèse.

Selon Czàràn (1998), les trois hypothèses de base des modèles de dynamique de population négligeant l'espace sont : (i) l'hypothèse d'abondance, selon laquelle les populations sont composées d'un grand nombre d'individus ; (ii) l'hypothèse d'uniformité, supposant que tous les individus d'une même population sont identiques ; (iii) l'hypothèse d'ergodicité, selon laquelle chaque individu bouge très vite et indépendamment des autres, conduisant à une parfaite homogénéité spatiale.

Dans le cas de *C. sordidus*, l'hypothèse d'abondance n'est pas respectée car c'est un insecte de type 'K', avec une faible fécondité (Cuillé 1950; Gold et al. 2001), le nombre d'individus par hectare se compte en dizaines de milliers (Delattre 1980) lorsque les parcelles sont très infestées, contrairement à d'autres espèces de type 'r' comme les pucerons pour lesquelles les densités de populations se comptent en millions. Concernant l'hypothèse d'uniformité, l'expérience conduite sur la dispersion du charançon a montré une forte variabilité des comportements individuels des adultes. Par ailleurs, il a fallu intégrer dans le modèle l'ensemble des stades de développement du charançon qui ont des comportements de déplacement différents : œuf, immobile ; larve, se développant uniquement sur un organe immobile ; et adulte pouvant se déplacer. La condition d'ergodicité n'est pas non plus respectée car l'expérience de télémétrie prouve que le charançon a des capacités de déplacement limitées. L'intérêt de construire un modèle spatial est donc confirmé.

Les simulations du modèle, ainsi que l'expérience de télémétrie ont montré que l'insecte était sensible à une modification de la configuration spatiale des parcelles de

bananiers. Il apparaît donc nécessaire de figurer explicitement l'ensemble des habitats dans le modèle.

Reste la question du choix de l'approche individu-centrée. Cette approche est intéressante dans la mesure où elle permet de faire émerger des propriétés populationnelles à partir de processus individuels, c'est-à-dire des propriétés autres que celles directement intégrées dans le modèle. La meilleure manière de juger si cette approche était la plus pertinente eut été de construire un modèle agrégé, non individu-centré, pour examiner les capacités de ce dernier à reproduire les patterns du modèle individu-centré. En l'absence de modèle de ce type sur charançon, on peut supposer que certains patterns comme l'augmentation des dégâts dans les bananeraies désynchronisées sont dus aux probabilités individuelles de trouver un bananier à un stade favorable pour la ponte (cf. Chapitre V). Les patterns d'utilisation de l'espace (Chapitre IV) sont également dus aux déplacements individuels. Par contre, d'autres patterns comme l'augmentation de la durée d'infestation d'une parcelle plantée en groupe (cf. Chapitre V) pourraient être reproduits avec un modèle de type Coupled Map Lattice voire automate cellulaire. Le modèle défini dans la thèse possède une résolution suffisante pour répondre à toutes les questions générées par l'objectif de la thèse, mais pas toujours nécessaire dans la mesure où des modèles plus agrégés permettraient de répondre à certaines questions. Son principal avantage est d'offrir une plasticité suffisante pour s'adapter à de nombreuses situations.

3. Perspectives

3.1. La fonction de dispersion de COSMOS : quels mécanismes sous-jacents et quelle valeur générale?

En proposant une décomposition du mouvement selon l'habitat, cette thèse apporte des éléments de réponse en écologie animale sur les mécanismes de mouvement et de sélection d'habitat par les organismes. Ces aspects peuvent être traités de manière plus fine, en s'appuyant sur des outils d'écologie du comportement, en tentant de comprendre comment l'organisme traite l'information disponible sur son environnement lorsqu'il se déplace. Les écologistes et les comportementaux travaillant généralement à des échelles spatiales différentes, trouver les mécanismes comportementaux expliquant les patterns de mouvement observés à une large échelle spatiale permettrait de créer des points de contacts entre les deux disciplines. Les raisons pour lesquelles un individu stationne dans tel ou tel élément d'habitat sont liées aux propriétés de l'élément qui peut se comporter comme (i) une barrière physique aux stimuli chimiques ou (ii) une protection contre les prédateurs. Dans le cas du charançon, il serait intéressant d'évaluer la part de ces deux propriétés pour chaque élément d'habitat, en utilisant des outils d'électrophysiologie (Zhou et al. 2009) déjà employés sur insectes volants.

Le modèle COSMOS peut s'appliquer à d'autres insectes, voire d'autres organismes vivants. La fonction de déplacement est adaptable à n'importe quel organisme se déplaçant

dans un milieu hétérogène et qui s'oriente selon des stimuli chimiques provenant de son environnement. Il est ainsi possible d'importer une carte SIG (format raster) des éléments du paysage ayant chacun un potentiel dépendant de l'espèce étudiée. Il sera possible de simuler le déplacement d'un individu ou d'une population dans ce paysage, en fonction de ces potentiels.

Par exemple, le modèle est actuellement en cours d'application à la dynamique spatiale d'*Helicoverpa zea*, lépidoptère ravageur des tomates. De même que *C. sordidus*, *H. zea* présente une spatialisation importante des attaques. Par contre, il possède des capacités de dispersion plus élevées (par le vol). Dans ce cadre, sa perception de l'espace n'est *a priori* pas dépendante de l'habitat de résidence et donc seuls les potentiels de préférence des habitats devront être considérés dans le modèle. *H. zea* possède une plus grande gamme d'hôte que *C. sordidus*, incluant le maïs. Dans le cadre de l'introduction d'une bande de maïs au sein d'une parcelle de tomate (considérée comme une bande piège), il s'avère que le maïs et la tomate sont attractifs pour *H. zea* uniquement en stade de floraison. Le modèle COSMOS pourrait servir à tester comment organiser dans l'espace et dans le temps les bandes de maïs dans une parcelle de tomate afin de limiter les attaques de *H. zea* sur tomate.

3.2. Gestion du charançon du bananier en fonction de sa plante-hôte

Le modèle COSMOS a révélé l'importance de l'organisation de la plantation, du piégeage et des jachères sur les populations de charançons (**Figure VII-1**). Au Chapitre V, les simulations ont révélé un effet positif de la désynchronisation des bananiers sur les populations de charançons. Dans une perspective de limitation de ces dernières, les planteurs doivent veiller à maintenir leurs bananeraies synchronisées. Par ailleurs, le schéma de plantation influe sur la progression des attaques de charançons, mais également sur l'intensité des attaques. Il est préférable de favoriser la plantation régulière ou en double rang pour des parcelles de bananiers plantées sur une courte période, et de réserver la plantation en groupes à des bananeraies non contaminées plantées à proximité de parcelles contaminées, afin de limiter la progression des charançons. Au Chapitre VI, on a constaté qu'il était plus intéressant de disposer les pièges à l'interface entre les jachères et les plantations de bananiers pour augmenter l'efficacité du piégeage. Dans le cas d'une replantation sur une parcelle déjà contaminée, il est préférable de ne pas fractionner la surface en bananes pour limiter les populations de charançons. Ces propositions issues de simulations du modèle doivent être testées au champ afin d'être validées par les planteurs, aussi bien en termes d'efficacité sur le charançon, mais également d'organisation et de temps de travail supplémentaires. Par exemple, la limitation de la fragmentation de la zone de bananeraie sera rendue difficile dans un parcellaire très morcelé par des éléments non cultivables, tels que ravines ou haies. D'autre part, varier les schémas de plantations suivant les parcelles peut compliquer l'organisation du travail du planteur à l'échelle du réseau de parcelles. Enfin, le maintien de la synchronisation des bananiers et par conséquent la réduction de la période de récolte entraîne une surcharge de

travail des ouvriers pendant la récolte. A l'inverse, une bananeraie désynchronisée offre une période de récolte étalée sur toute l'année.

L'utilisation de variétés résistantes (**Figure VII-1**) au charançon n'a pas été développée dans la thèse, bien que les données existent sur la variation des traits de vie du charançon en fonction des variétés (Kiggundu et al. 2007). Il serait intéressant d'évaluer l'effet des variétés résistantes sur la dynamique des populations. Par exemple, dans les conditions de culture africaines où les variétés de bananiers sont différentes à l'échelle intraparcellaire, comment organiser spatialement le mélange variétal pour limiter les populations de *C. sordidus*? D'autre part, en considérant uniquement l'aspect cumulatif des dégâts dans les bulbes de bananiers, il serait intéressant d'étudier la relation entre la longueur du cycle de chaque variété de bananier et les niveaux d'attaques. Comme les durées de cycle sont très variables suivant les variétés, il est possible que les variétés les plus sensibles au charançon soient celles qui ont le plus long cycle de développement. Par conséquent le niveau de résistance pourrait en grande partie être expliqué par cette variable.

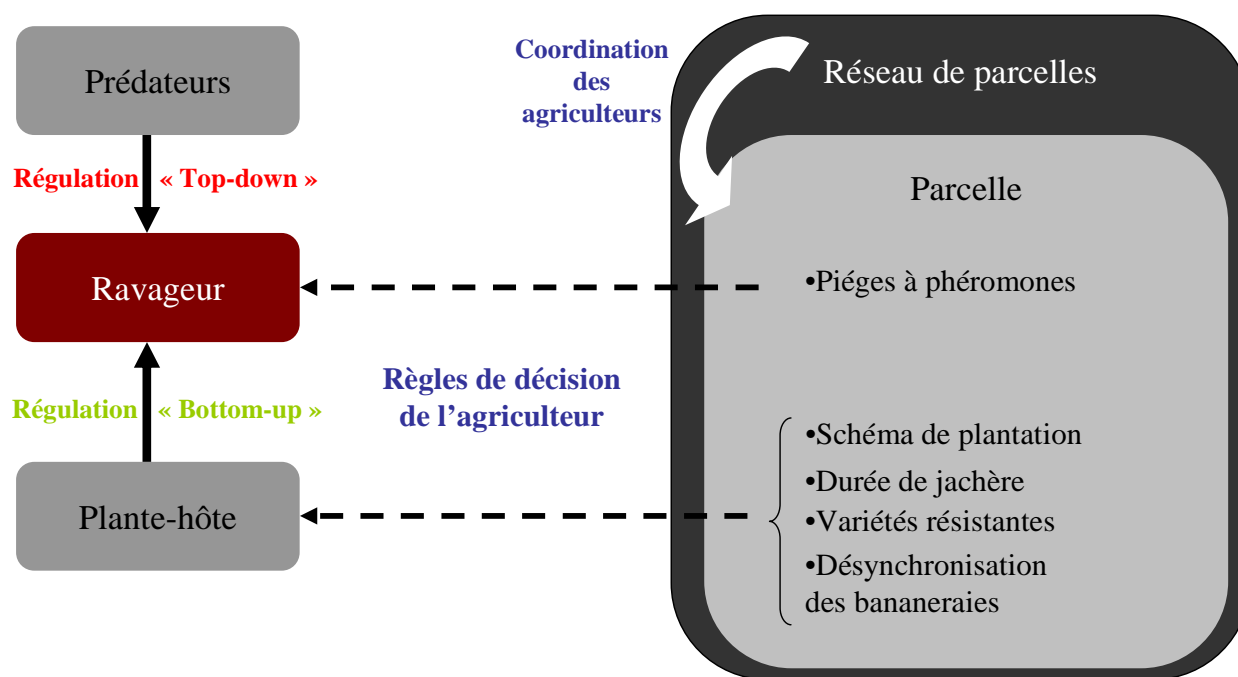


Figure VII-1. Schéma général de l'ensemble des processus pouvant être intégrés dans le modèle COSMOS en écologie des réseaux trophiques (rouge), en agronomie (vert clair) et socio-économie (bleu foncé).

Certains paramètres biologiques nécessitent d'être estimés plus précisément afin de rendre le modèle COSMOS plus réaliste. En particulier, l'habitat dépendance telle qu'intégrée dans le modèle se réfère au mouvement et à la ponte des femelles. Or la mortalité des adultes peut également dépendre des conditions de milieu. Des milieux hostiles, tels que sol nu ou ravines, risquent d'augmenter la probabilité de prédation et la mort par dessiccation des individus soumis à une hygrométrie plus faible qu'en bananeraie. Il serait donc intéressant de

réaliser des expérimentations en ce sens en utilisant la technique RFID pour évaluer des taux de mortalité variables suivant le milieu (**Tableau VII-1**).

Au vu des résultats de l'analyse de sensibilité du Chapitre V, certains paramètres et processus démographiques affectent particulièrement la dynamique d'infestation de *C. sordidus* (**Tableau VII-1**). Le modèle a mis en évidence certaines carences dans l'estimation de la gamme de variabilité de ces paramètres sensibles. Il est nécessaire de conduire des études de laboratoire supplémentaires pour bien estimer ces paramètres. Des études ont été mises en place au début 2010 pour estimer la longévité et la fécondité de *C. sordidus* en fonction de la température, en élevant des cohortes d'adultes d'âge connu dans trois chambres climatiques réglées à 15, 20 et 25°C. Les traits de vie découlant de ces études sont spécifiques de l'espèce. Intégrés au modèle COSMOS, ils permettront une plus grande généricité du modèle à d'autres conditions climatiques que celles des Antilles.

3.3. Gestion du charançon du bananier en fonction de ses prédateurs ou parasites potentiels

Le modèle COSMOS est également un outil exploratoire permettant de tester "virtuellement" dans un premier temps des nouvelles stratégies de lutte contre le charançon (**Figure VII-1**). Une approche prometteuse porte sur l'association entre un parasite et un piège à phéromone. Le nématode entomopathogène (Padilla-Cubas et al. 2010) et le champignon *Beauveria bassiana* (Akello et al. 2010) sont de bons candidats. La technique consiste à placer des pièges avec phéromone remplis de parasites, où les charançons viennent s'infecter puis repartent contaminer leurs congénères. Très peu d'études existent sur le sujet et le modèle COSMOS pourrait apporter des premiers éléments de réponse sur la validité de cette approche, moyennant quelques expérimentations supplémentaires qui sont exposées dans le **Tableau VII-1**. En effet, il est nécessaire de connaître la probabilité de contamination de proche en proche lorsque les individus se regroupent. D'autre part, la probabilité de contamination des adultes par les parasites est un critère clef à évaluer, de même que le temps de latence entre la contamination et la mort des individus. Ces paramètres peuvent être évalués au laboratoire sans l'aide des puces RFID. Comme les deux parasites concernés (nématode entomopathogène et *Beauveria bassiana*) ont des profils épidémiologiques très différents, le modèle COSMOS peut comparer leur efficacité respective dans des conditions au champ "virtuelles".

Tableau VII-1. Récapitulatif des connaissances manquantes et leur utilisation

Connaissances à acquérir	Utilisation
<u>En laboratoire:</u>	
Longévité, fécondité des adultes en fonction de la température.	Meilleure estimation des intensités d'attaques.
Probabilité de contamination des adultes par les parasites.	Modélisation de l'association parasite/piège à phéromone.
Probabilité de contamination des adultes de proche en proche.	<i>Idem.</i>
<u>Au champ:</u>	
Mortalité des adultes en fonction de leur habitat.	Meilleure estimation des distributions spatiales des populations en environnement hétérogène.
Effet des variables climatiques sur l'efficacité du piégeage.	Possibilité de valider le modèle à l'échelle d'un réseau de parcelles piégées.
Estimation de l'efficacité du piégeage par morceaux de pseudo troncs.	Utilisation du modèle en Afrique.
Estimation du rôle des prédateurs potentiels du charançon et quantification des taux de prédateurs.	Modélisation multi-trophique du complexe bananier-charançon-prédateur.

Plus généralement, dans le domaine de l'écologie des réseaux trophiques, la question générale de la part des processus spatiaux dans la régulation d'un ravageur par ses ennemis est ouverte. En effet, la prédation d'un organisme par un autre est dépendante de l'abondance et de la dynamique spatiale des proies, des prédateurs et de la stratégie d'exploitation des proies par les prédateurs. Comment relier des mesures de déplacement ou d'occurrence spatiale de prédateurs à des pressions de prédation exercées sur un ravageur? Comment l'organisation spatiale des ressources modifie le réseau trophique d'un agroécosystème? Coupler des techniques de suivi par télémétrie à un modèle de simulation spatialement explicite permettrait de mieux comprendre les mécanismes d'interaction trophiques au sein des agroécosystèmes. Le modèle intégrerait l'ensemble des processus spatiaux d'intérêt dans le fonctionnement du réseau trophique, et permettrait de tester si les fonctions de régulations des bioagresseurs varient avec l'organisation spatiale des ressources basales des réseaux trophiques. Une simplification des espèces en groupes trophiques (ensemble des taxa ayant un régime alimentaire similaire) est nécessaire pour intégrer la notion de réseau trophique dans des modèles spatialisés (Caron-Lormier et al. 2009). Dans le cas des groupes trophiques de prédateurs, il sera nécessaire de modéliser leur comportement de recherche des proies réparties de manière hétérogène dans l'environnement. On pourra s'appuyer sur les théories de recherche optimale de ressource où l'espace est considéré implicitement ["optimal foraging

behavior" développée par Charnov (1976)] ou explicitement [distribution optimale des prédateurs pour exploiter une proie (Viswanathan et al. 1999)].

Ainsi, une thèse est actuellement en cours (Grégory Mollot, 2009-2012) afin d'estimer les capacités de contrôle de *C. sordidus* par des prédateurs potentiels. Dans ce cadre, le doctorant estime les taux de prédation instantanés des œufs de charançons par les fourmis, et la variation spatiale des densités de fourmis dans les parcelles. Pour intégrer ces paramètres dans le modèle COSMOS (**Tableau VII-1**), il sera nécessaire d'ajuster la résolution temporelle et surtout spatiale du modèle en fonction de l'échelle spatiale d'interaction entre fourmis et charançons. Les statistiques spatiales appliquées aux densités de fourmis estimées permettront de définir la taille des foyers de fourmis, et ainsi l'échelle spatiale à considérer dans le modèle. Les puces RFID peuvent également servir à estimer le rayon d'action des fourmis: en plaçant régulièrement des puces RFID enduites d'attractif alimentaire, celles-ci seront ramenées par les fourmis au nid. Sous réserve que les puces n'ont pas été enfouies trop profondément dans le nid pour ne plus être détectées, il est ainsi possible d'estimer la distance entre le nid et la position initiale de la puce et donc la surface d'approvisionnement des fourmis.

L'étude de télémétrie (Chapitre III) a révélé quelques cas de prédation de *C. sordidus* par des crapauds-buffles (*Bufo marinus*). Il serait intéressant d'évaluer l'impact de cette prédation en marquant des crapauds et des charançons avec des puces RFID (avec une fréquence différente pour chaque espèce) dans une parcelle afin de suivre leurs déplacements. La différence de fréquence permettrait de détecter les crapauds ayant ingéré des charançons. En analysant les trajectoires de chaque espèce, il serait également possible de calculer les probabilités d'intersection des trajectoires entre le prédateur et sa proie, et ainsi la pression de prédation de *B. marinus* sur *C. sordidus*.

3.4. Gestion du charançon du bananier en fonction des règles de décision des agriculteurs

Dans le domaine de l'agronomie, la thèse ouvre la question de l'utilisation des modèles pour analyser l'effet des pratiques culturales sur les populations de ravageurs. Le modèle devient ici une plateforme de simulation prenant en compte les interactions avec le système décisionnel de l'agriculteur (**Figure VII-1**). Comment considérer les décisions individuelles des agriculteurs pour chaque parcelle dans le contrôle des populations de ravageurs à l'échelle du réseau de parcelles? A quelle échelle d'espace et de temps doivent se coordonner les actions des agriculteurs pour limiter les populations?

Le modèle COSMOS peut apporter des éléments de réponse à ces questions, à condition d'y intégrer les règles de décision des planteurs à l'échelle parcellaire. Ce travail pourrait se faire en collaboration avec l'équipe GREEN du CIRAD. Pour ce faire, il serait nécessaire de valider le modèle à l'échelle du réseau de parcelles, ce qui est rendu possible par

l'existence d'une base de données idoine. Ensuite, plusieurs acteurs seraient ajoutés au modèle avec leurs propres règles de décision. Celles-ci porteraient sur l'utilisation et la durée des mises en jachère, les schémas de plantations, l'utilisation ou non de pièges à différentes densités et selon des arrangements spatiaux variables. Chaque acteur aurait pour but de limiter les populations de ravageurs dans sa parcelle. Une enquête auprès des planteurs compléterait un travail déjà réalisé sur l'organisation spatiale de l'activité agricole (Houdart 2005) pour réaliser une typologie des pratiques agricoles en bananeraie et formaliser les règles de décision selon les classes obtenues .

4. Conclusion générale

Un nombre croissant de modèles théoriques souligne l'importance de la distribution spatiale des populations (Tilman and Kareiva 1997). Néanmoins, cette "théorie spatiale" souffre d'un manque de recherche empirique pour l'étayer. Faire le lien entre processus et pattern nécessite de mesurer le processus en cause, ce qui est souvent difficile et coûteux (McIntire and Fajardo 2009). Ma thèse a tenté de mobiliser l'ensemble des outils disponibles en écologie spatiale pour étayer certains aspects de la "théorie spatiale", avec un accent particulier sur l'étude du mouvement. Elle a testé des hypothèses simples de processus écologiques pour comprendre des patterns spatiaux (Fortin and Dale 2005), selon la notion de "Pattern-oriented modelling" telle que décrite par Grimm et al. (2005). Ma thèse se situe à l'interface entre écologie et agronomie dans le sens où elle a hiérarchisé et analysé les processus écologiques expliquant les niveaux de populations d'un ravageur, afin de s'en servir comme leviers pour limiter ses dégâts au champ. Elle postule qu'une modification du milieu affectant un processus écologique sera plus difficile à contourner par le ravageur, en particulier si le processus écologique en cause (e.g. le comportement de ponte) est critique en termes de survie ou de reproduction dans les conditions normales (Roitberg 2007). Elle a proposé un modèle mécaniste permet de quantifier le poids de chaque processus dans l'explication d'une variable épidémiologique, en l'occurrence ici la pression de *C. sordidus* sur sa plante hôte. Ce modèle est un outil pour analyser des scénarii de configuration spatiale des éléments d'habitat influençant les déplacements, la démographie et la dynamique d'infestation d'un ravageur, et pour sélectionner sur ces bases des agencements permettant de limiter son impact.

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Kilgore: Smell that? You smell that?

Lance: What?

Kilgore: A new computer, son. Nothing else in the world smells like that.

[kneels]

Kilgore: I love the smell of a new computer in the morning. You know, one time we had a simulation, for twelve hours. When it was all over, I turned it off. Smelled like...

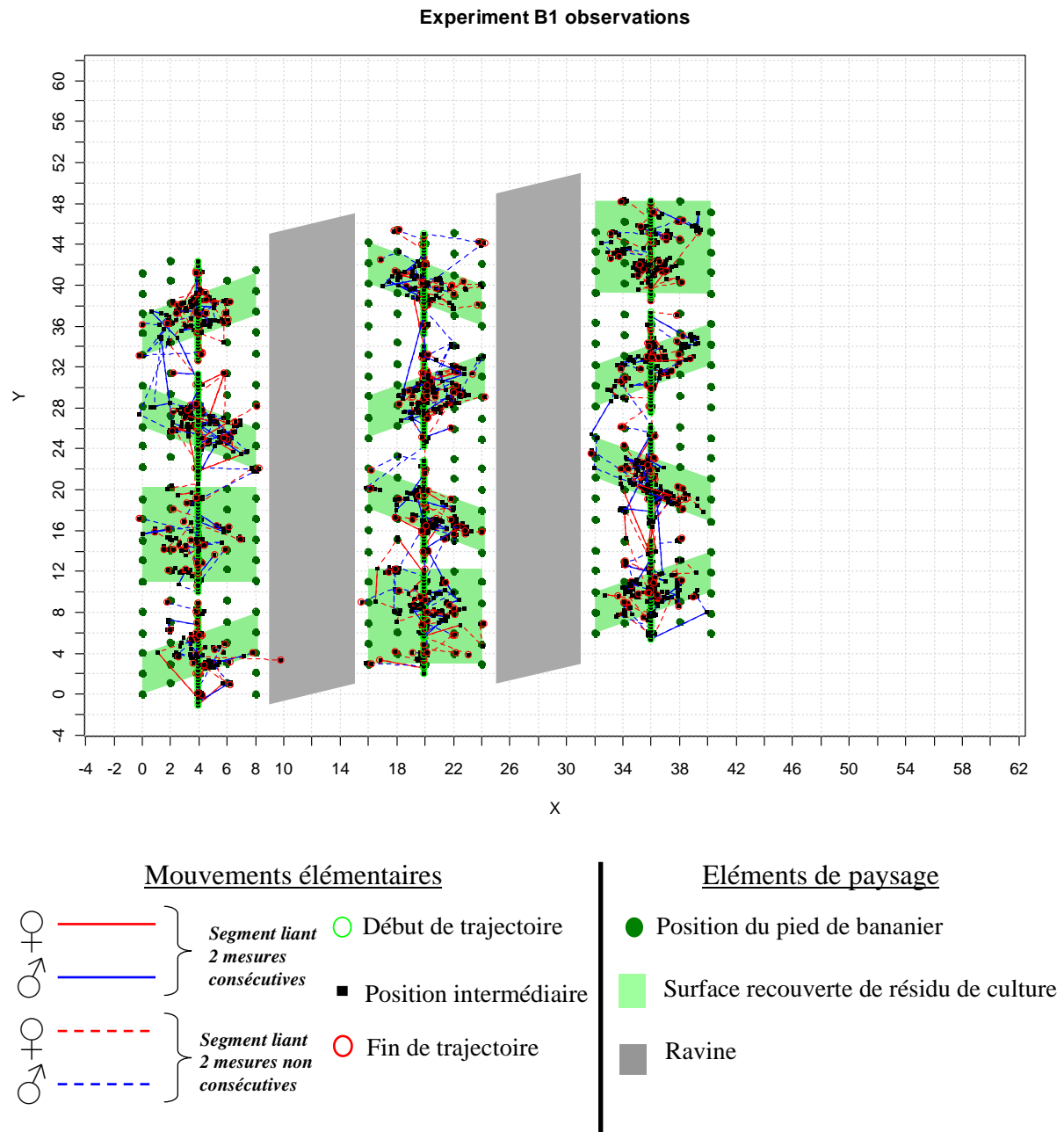
[sniffing, pondering]

Kilgore: ... publication. Someday this thesis' gonna end...

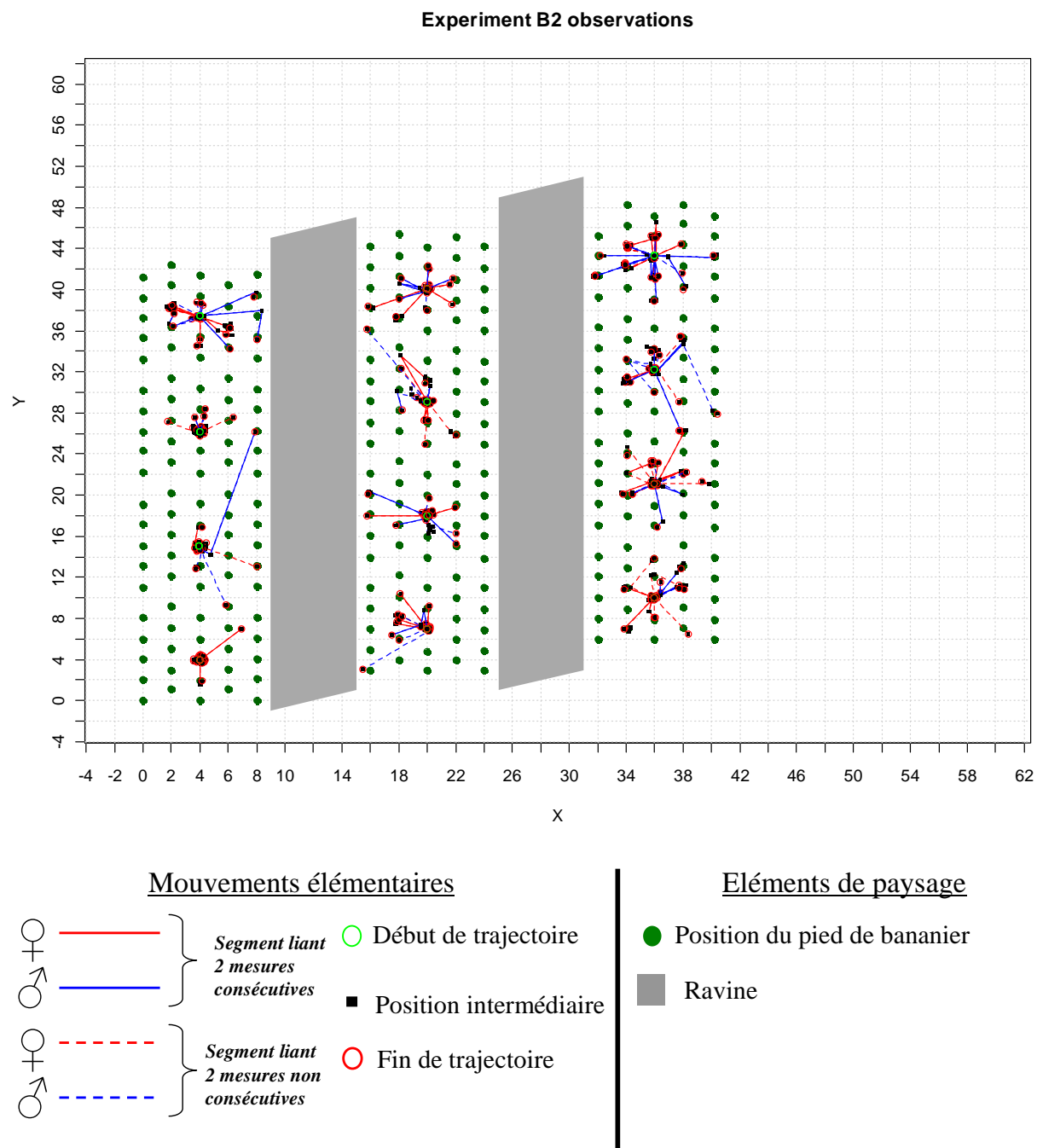
[suddenly walks off]

Adapté d'Apocalypse now, 1979

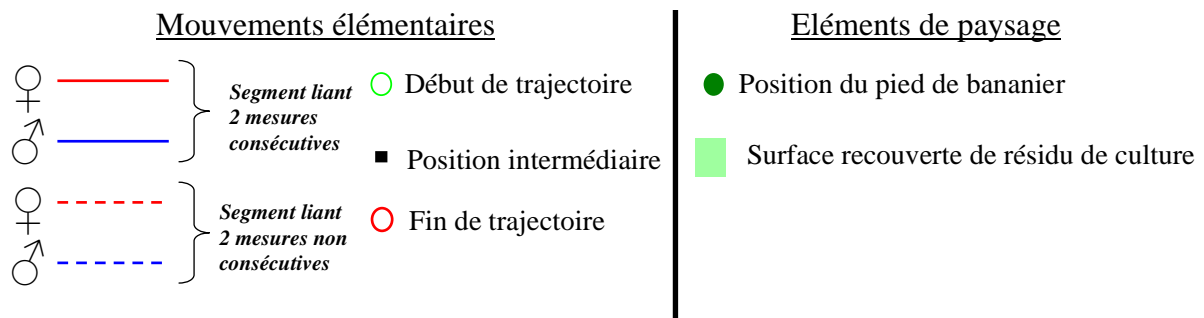
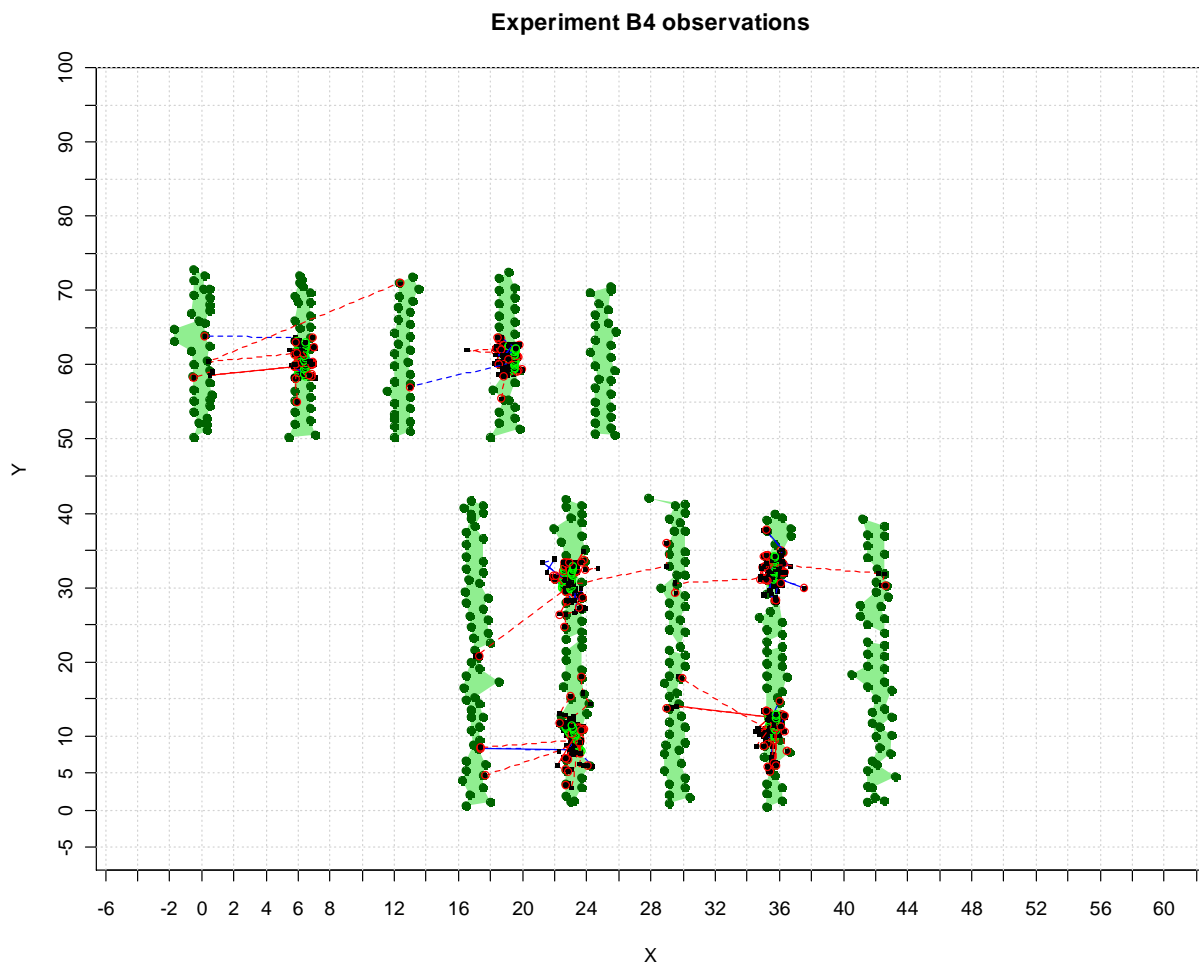
ANNEXE A. CARACTERISTIQUES DES ESSAIS SUR LE MOUVEMENT ET CARTOGRAPHIE DES TRAJECTOIRES DE CHARANÇONS.



Cartographies réalisées avec le logiciel R (package spatstat)

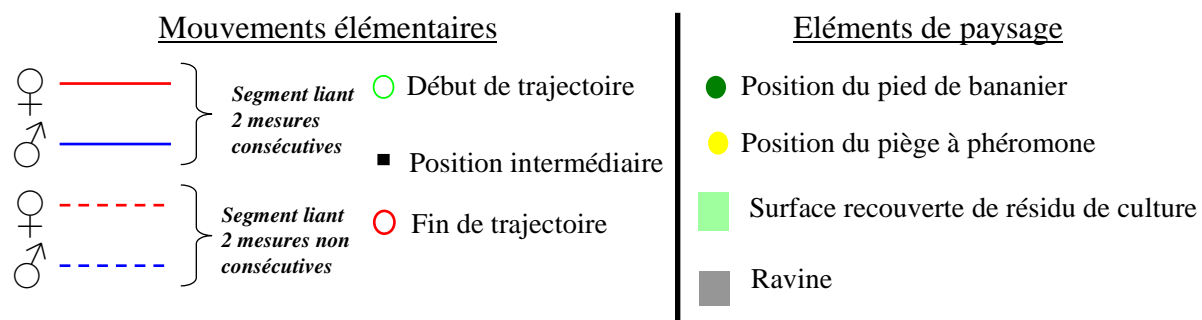
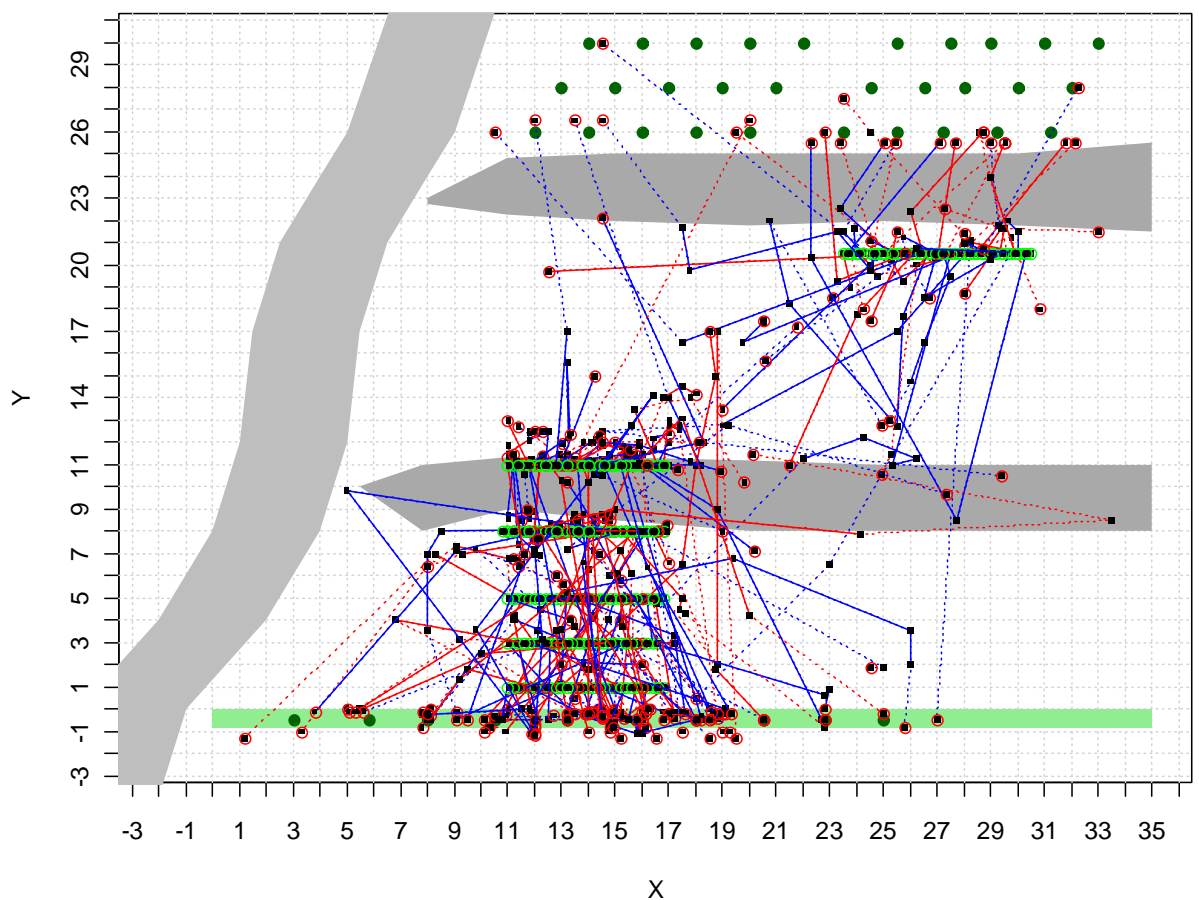


Cartographies réalisées avec le logiciel R (package spatstat)

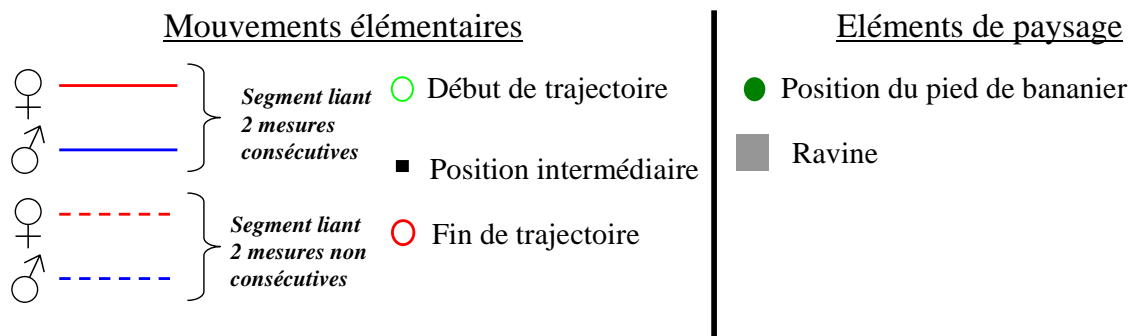
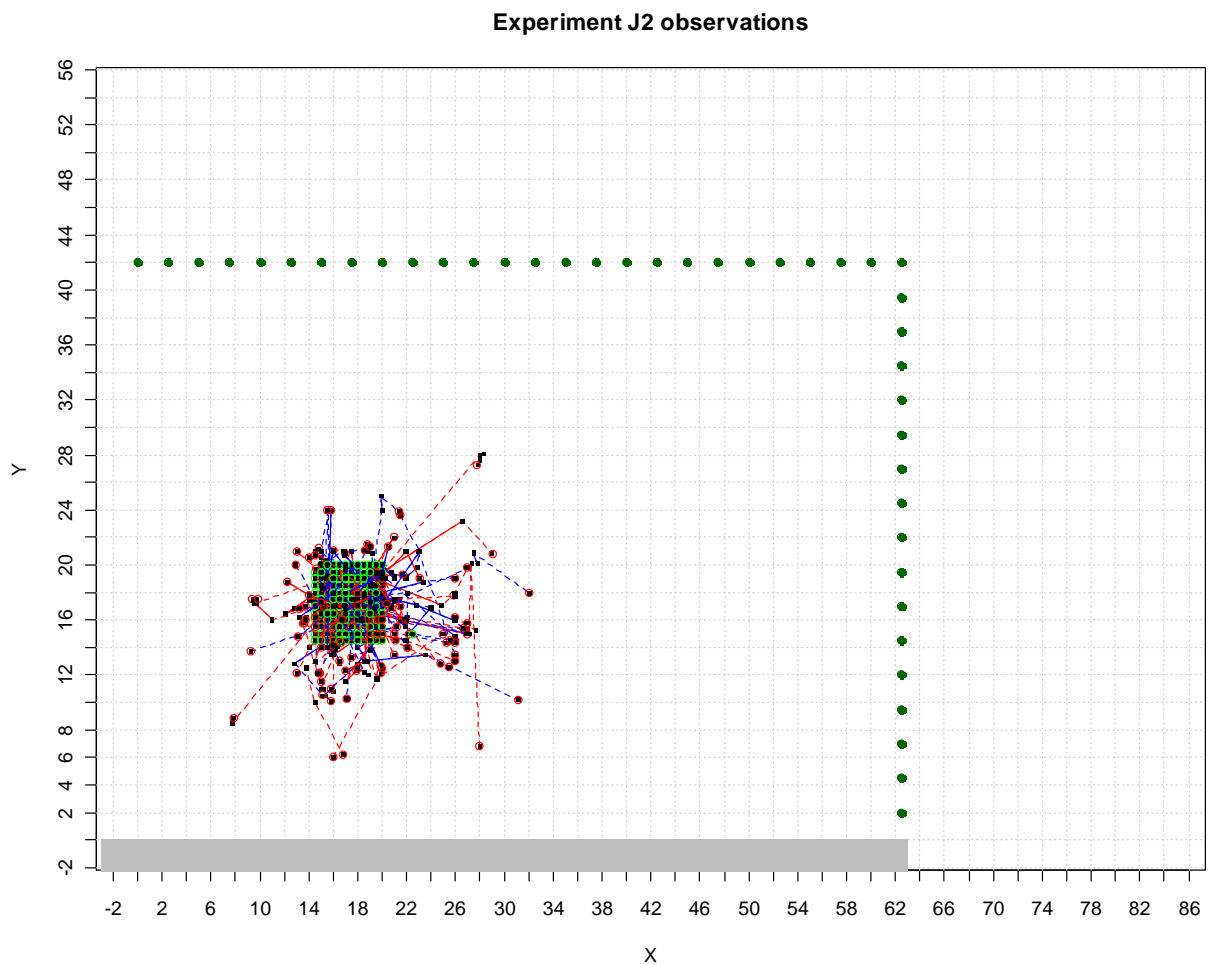


Cartographies réalisées avec le logiciel R (package spatstat)

Experiment J1 observations

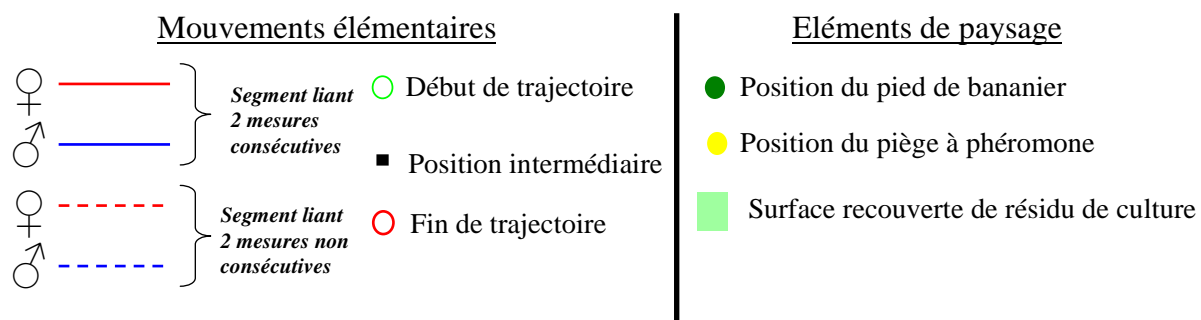
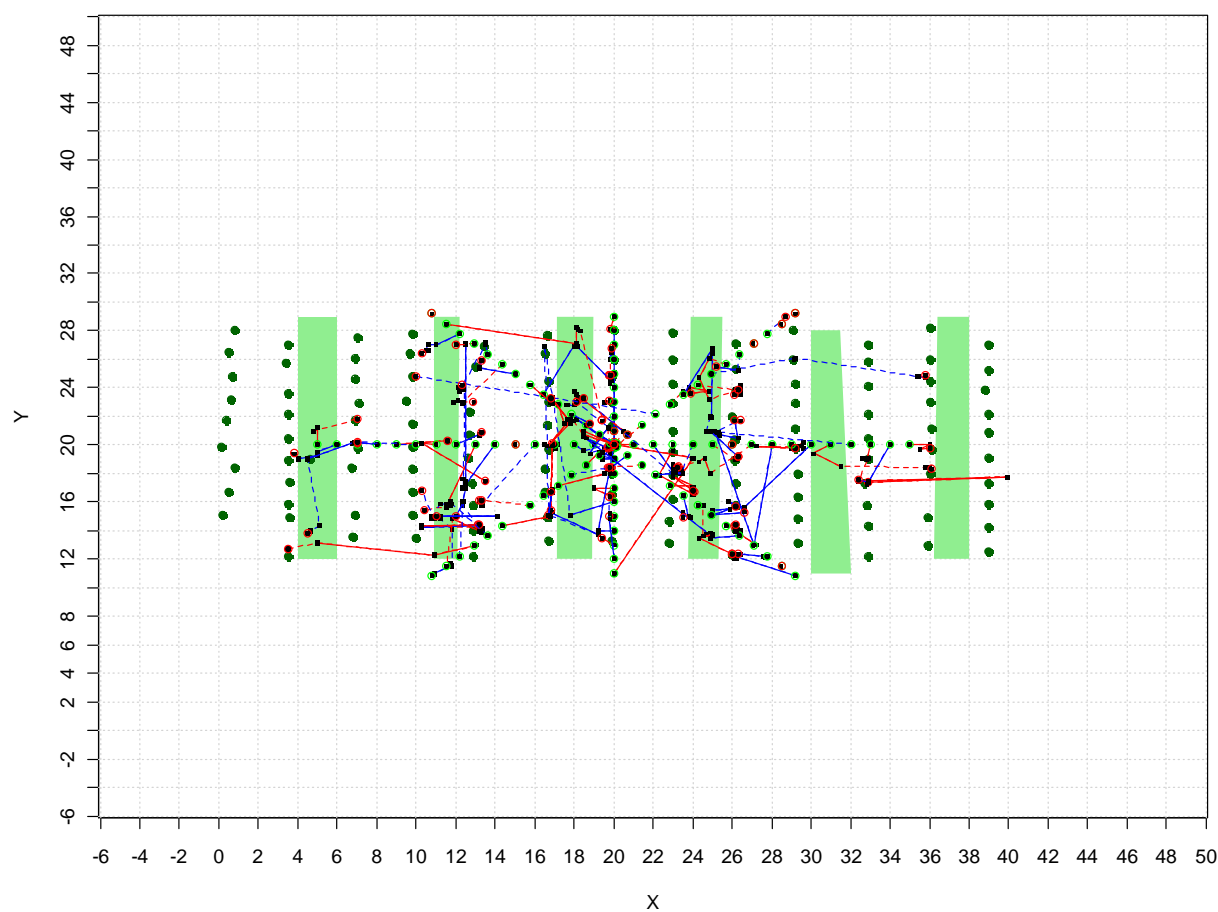


Cartographies réalisées avec le logiciel R (package spatstat)

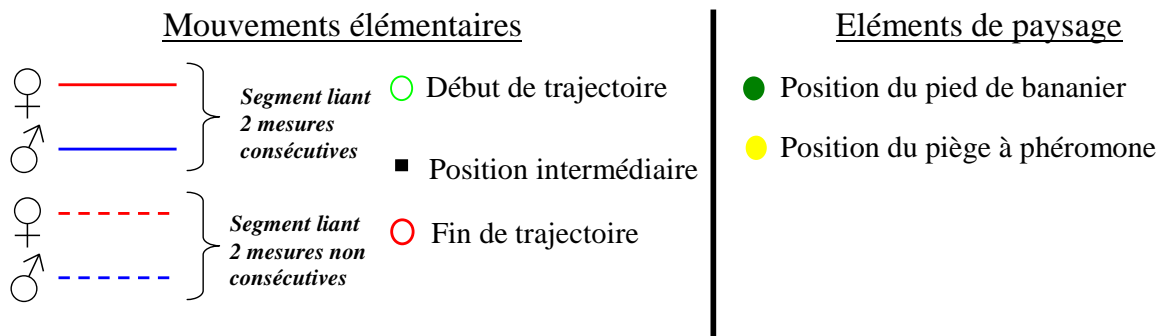
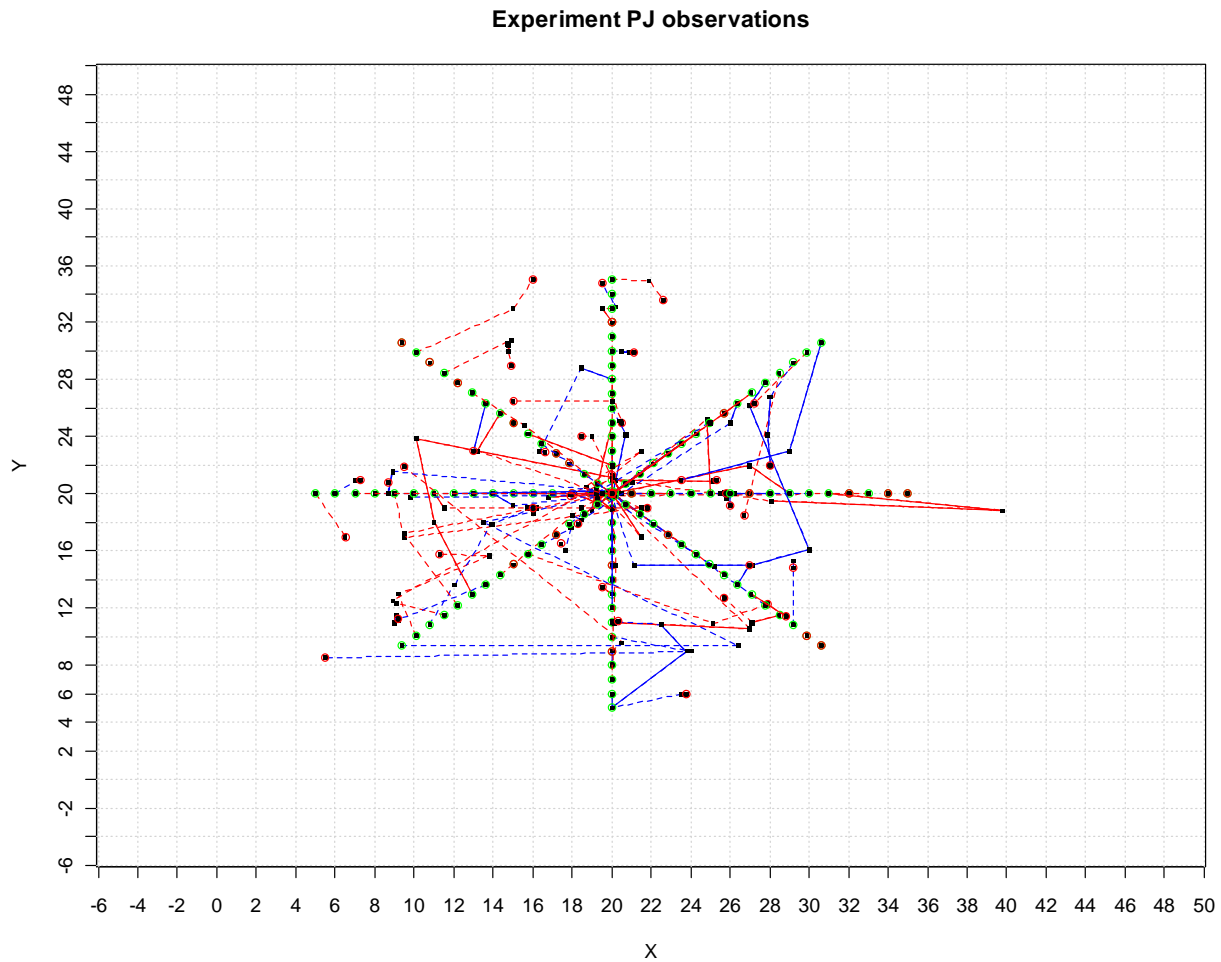


Cartographies réalisées avec le logiciel R (package spatstat)

Experiment PB observations



Cartographies réalisées avec le logiciel R (package spatstat)



Cartographies réalisées avec le logiciel R (package spatstat)

ANNEXE B. COMPARAISON DES DEUX VERSIONS DU MODELE COSMOS

On définira par COSMOS 1.0 la version du modèle incluant le mouvement défini dans le Chapitre V et par COSMOS 2.0 le modèle incluant le mouvement exposé dans les Chapitres IV et VI.

Calcul des indices

L'adéquation entre l'observé et la moyenne des simulés a été évaluée en calculant le "relative root mean squared error" (RRMSE) et l'efficacité de modélisation (EF) :

$$RRMSE = \frac{1}{\bar{y}} \sqrt{\frac{\sum_{i=1}^N (y_i - \hat{y}_i)^2}{N}} \quad EF = 1 - \sqrt{\frac{\sum_{i=1}^N (y_i - \hat{y}_i)^2}{\sum_{i=1}^N (y_i - \bar{y})^2}}$$

où y_i est la valeur observée de la sortie i , \hat{y}_i la valeur correspondante simulée par le modèle, \bar{y} la moyenne des y_i et N le nombre d'observations.

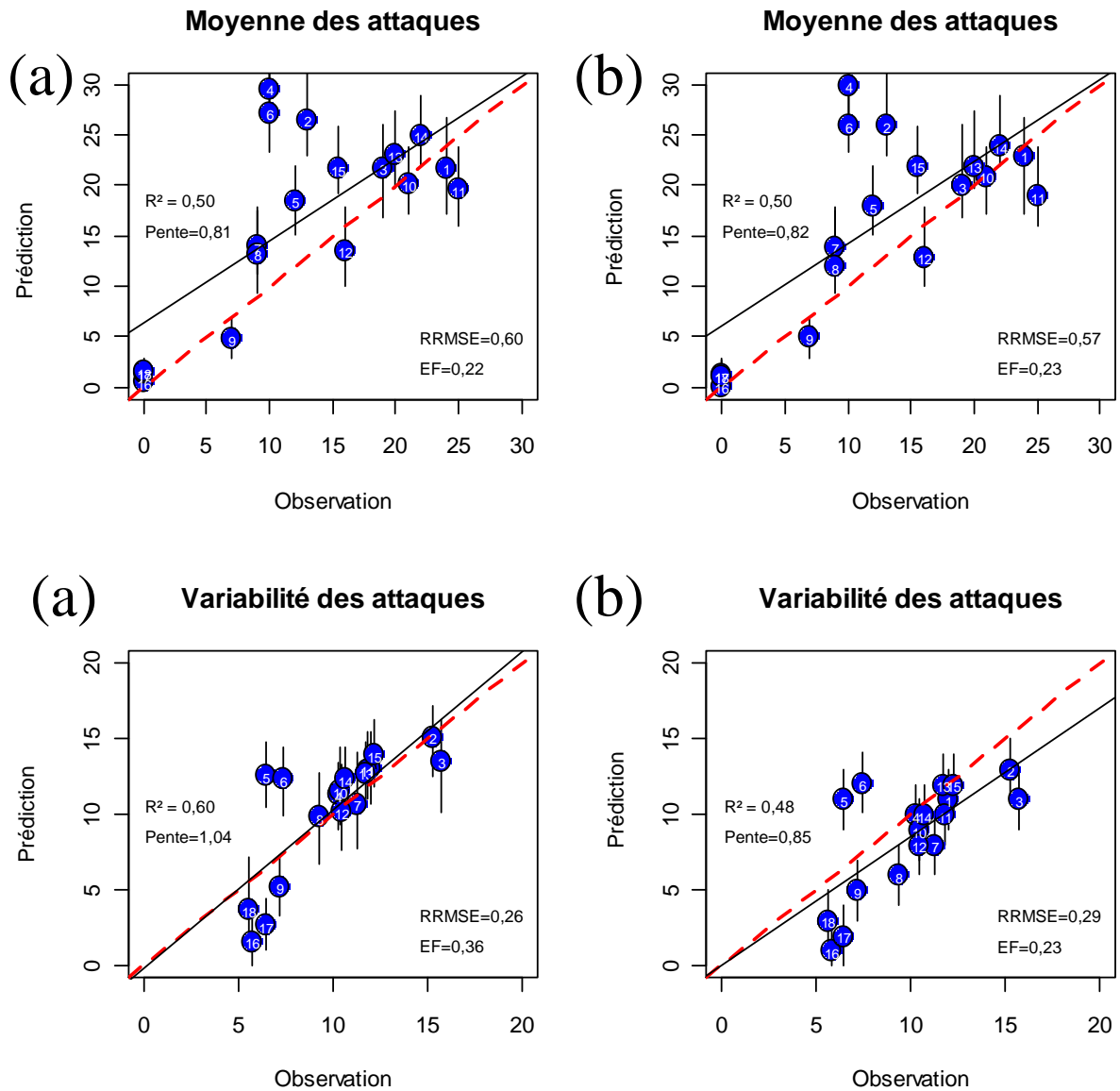


Figure B1. Comparaison des modèles COSMOS 1.0 (a) et COSMOS 2.0 (b) pour deux paramètres de la distribution des attaques dans chaque microparcelle (moyenne et écart-type en cm de circonférence attaquée). Les barres verticales indiquent les quantiles 0.975 et 0.025 issus de 100 simulations. La diagonale (tiret rouge pointillé) indique une parfaite concordance entre observation et simulation. Les numéros inscrits dans les cercles identifient chaque microparcelle. Le RRMSE et l'EF sont présentés dans le côté droit du graphique. La droite (trait plein) représente la régression linéaire de X sur Y (avec le R^2 et la pente). Note: Toutes les ordonnées à l'origine des quatre régressions linéaires ne sont pas significativement différentes de 0 (t-test, P-value<0.05).

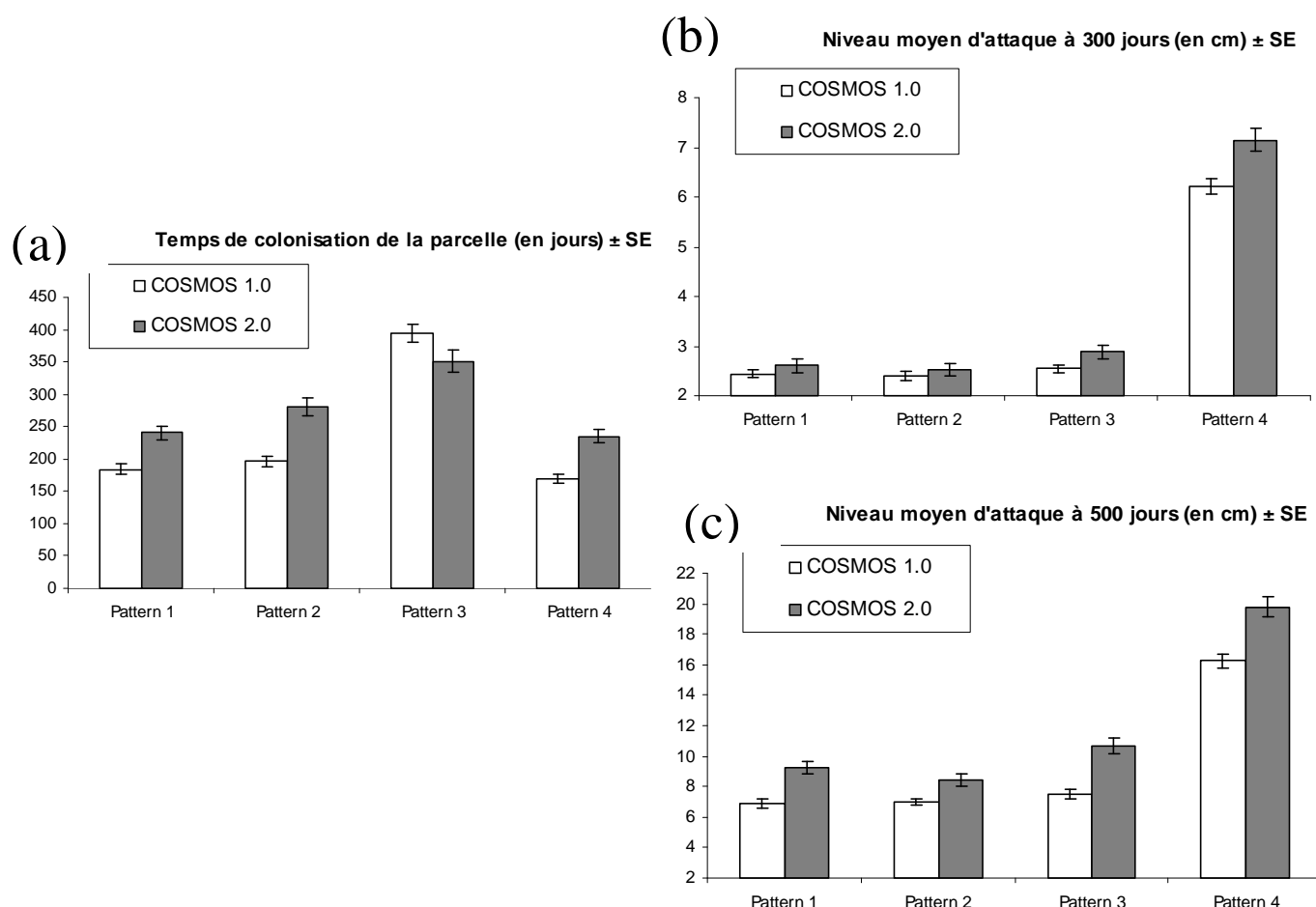


Figure B2. Graphique de comparaison des performances des modèles COSMOS 1.0 et COSMOS 2.0 vis-à-vis du temps de colonisation de la parcelle (a), du niveau moyen d'attaque à (b) 300 jours et, (c) 500 jours. Les barres verticales correspondent aux erreurs standards.

Comparaison des performances des deux modèles

La Figure B1 indique que les estimations des RRMSE et EF sont sensiblement les mêmes pour COSMOS 1.0 et COSMOS 2.0. Les valeurs des pentes des régressions linéaires indiquent une plus grande sous-estimation des variabilités des attaques pour le modèle COSMOS 2.0 que pour le COSMOS 1.0 [pente: 1.04 (COSMOS 1.0) et 0.85 (COSMOS 2.0), Figure B1]. Cette différence est probablement due à une fréquence de mouvement plus importante avec COSMOS 2.0.

La Figure B2 indique que le modèle COSMOS 2.0 présente les mêmes tendances que COSMOS 1.0. Le temps de colonisation est légèrement plus long excepté pour le pattern 3, avec pour conséquence un niveau moyen d'attaque dans les parcelles plus élevé, les charançons restant plus longtemps en moyenne sur chaque bananier. A noter qu'un temps de colonisation plus élevé n'est pas forcément lié à une fréquence plus élevée de mouvements.

ANNEXE C. COMPARAISON DES PERFORMANCES DU MODELE COSMOS EN LANGAGES SMALLTALK, R ET NETLOGO.

Présentation des langages

CORMAS ou Common-Pool Resources and Multi-Agents Systems est une plateforme de développement axée sur la construction de modèles de simulation basés sur le formalisme multi-agent et spécialisé dans le domaine de la gestion de ressources renouvelables par des individus ou groupes d'individus (Bousquet et al. 1998). Cette plateforme de simulation, téléchargeable sur <http://cormas.cirad.fr>, fonctionne sous VisualWorks, et permet de développer des applications en langage Smalltalk.

Netlogo est une interface de programmation individu-centrée réalisée par Uri Wilensky de Northwestern University. Elle est basée sur les logiciels Logo et Starlogo et écrite en Java et Scala.

R est un système d'analyse statistique et graphique créé par Ross Ihaka et Robert Gentleman. R est à la fois un logiciel et un langage qualifié de dialecte du langage S créé par AT&T Bell Laboratories. R est disponible sous plusieurs formes : le code (écrit principalement en C et certaines routines en Fortran), surtout pour les machines Unix et Linux, ou des exécutables précompilés pour Windows, Linux et Macintosh.

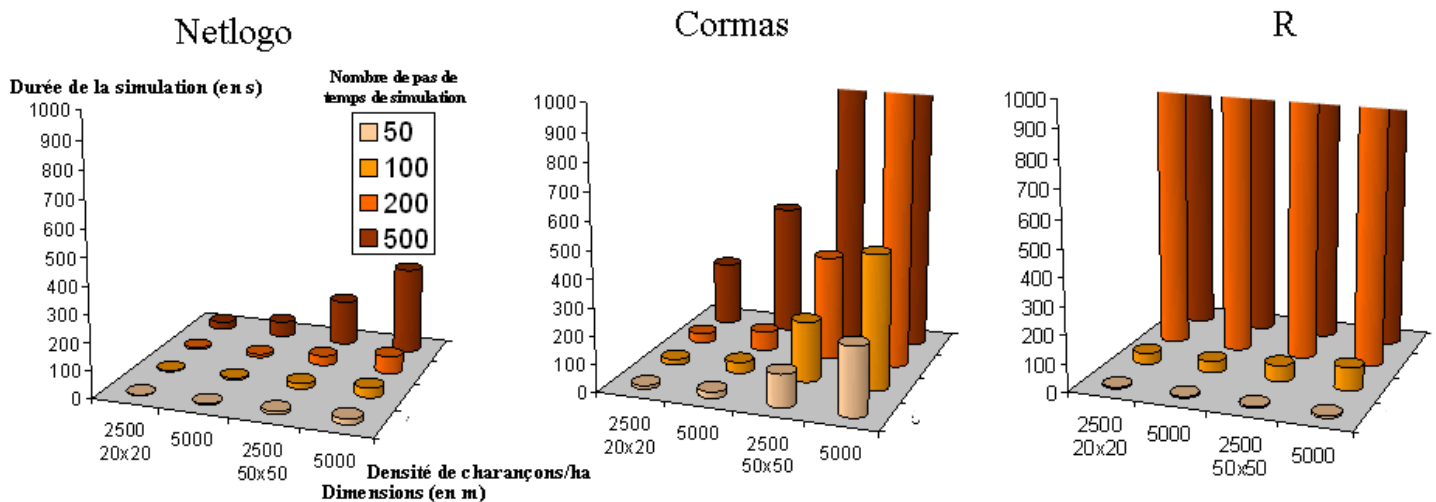


Figure C1. Comparaison des performances du modèle COSMOS programmé en Netlogo, Smalltalk et R. Toutes les simulations sont basées sur une plantation régulière de bananiers séparés par 2 mètres. Les charançons adultes sont disposés aléatoirement dans la parcelle. La durée de la simulation est chronométrée à partir de l'initialisation jusqu'au nombre de pas de temps défini (50, 100, 200 et 500 pas de temps). Les simulations ont été conduites pour deux densités de charançons à l'hectare (2500 et 5000 charançons à l'hectare) et deux tailles de grille différentes (carrés de 20 et 50 cellules de côté). Les simulations ont été réalisées avec un ordinateur portable Dell® (Windows XP SP2, Processeur Intel® CPU T2400 1.83 GHz, 0.99 Go de RAM). Note: le graphique est tronqué à 1000 secondes de simulation.

Comparaison des performances des langages

Pour le langage R de type indexé, le temps de calcul ne dépend pas de la densité de charançon ni de la taille de la grille. Par contre, il augmente considérablement à partir de 200 pas de temps, car il est nécessaire d'accumuler en mémoire l'ensemble des variables de la grille afin de tracer les graphiques en fin de simulation.

Les interfaces Netlogo et Cormas permettent de tracer en temps réel, toutes les variables de l'environnement. Le modèle programmé en Netlogo offre de bien meilleures performances que celui programmé en Smalltalk. Il est à noter que la programmation n'est pas optimisée dans tous les cas, et il est possible qu'un programmeur averti puisse améliorer les performances du modèle. Ayant travaillé dans le dernier chapitre (Chapitre VI) sur de grandes échelles spatiales, il m'est apparu nécessaire de reprogrammer le modèle COSMOS en Netlogo, langage présentant des performances accrues en terme de temps de calculs.

RESUME

Dynamique spatiale du charançon du bananier en interaction avec le système de culture et l'organisation paysagère. L'objectif de cette thèse est d'identifier et de comprendre les processus liant un ravageur à son habitat afin de limiter la population de ce ravageur. Deux approches peuvent permettre d'étudier l'hétérogénéité spatiale des populations d'une espèce: les statistiques appliquées à des données spatialisées et la modélisation mécaniste. Mon travail de thèse montre l'intérêt de combiner ces deux approches afin de comprendre l'interaction entre traits de vie et dynamique spatiale d'une population. Comprendre les comportements de dispersion nécessite de collecter des données spatiales à l'échelle de l'individu. En combinant une approche statistique par maximum de vraisemblance et un modèle mécaniste sur des données spatialisées que j'ai récoltées sur l'insecte par télémétrie RFID (Radio Frequency IDentification), j'ai montré une forte dépendance du déplacement vis-à-vis des éléments du paysage. Un modèle stochastique individu-centré (COSMOS) a été développé afin de simuler la propagation spatiale et les attaques du charançon en interaction avec les différents éléments du système de culture. Le modèle a été confronté avec succès à des données d'infestation réelles à l'échelle d'une parcelle de bananiers, en comparant les données d'infestation observées aux données simulées. Les propriétés émergentes du modèle ont été explorées en simulant des assemblages spatiaux de bananiers. Par exemple, le modèle a montré que la vitesse de colonisation d'une parcelle est plus importante lorsqu'elle est plantée de manière régulière plutôt qu'en groupes de bananiers. Le modèle a révélé l'importance de la zone de transition entre la bananeraie et la jachère pour l'optimisation du piégeage.

SUMMARY

Spatial dynamics of banana black weevil in relation with cropping system and landscape. The PhD work aims at detecting and understanding factors and mechanisms explaining the spatial heterogeneity of banana black weevils' (*Cosmopolites sordidus*) populations in order to control them. Two approaches are commonly considered to understand the spatial heterogeneity of populations: statistics applied to spatial data and mechanistic modelling. My PhD work considers the interest of combining those approaches to understand the movement processes of insect adults and the interaction between life traits and spatial dynamics of a population. Understanding movement processes requires collecting spatial data at the individual level. By combining a statistical approach by maximum likelihood estimation and a mechanistic individual-based model, I showed a high dependence of movement versus habitat matrix. I showed also that perception of space is less important for a weevil located on a banana plant or on crop residues than for a weevil located on bare soil or ditch. An individual-based model (COSMOS) was developed to simulate the spatial dispersion and infestation of *C. sordidus* in interaction with different elements of the cropping system. The model was successfully tested at the plot scale, by comparing infestation statistics between observed and simulated values. The emerging properties of the model were tested by simulating different spatial arrangements of banana plants. For instance, the model showed that the time to colonize a plot is longer when the plot is planted regularly than when it is planted in patches. The model revealed the importance of the interface between banana area and fallow for locating weevils' trap.